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LONDON: BENTLEY HOUSE

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THE
DIRECTIVENESS
OF
ORGANIC ACTIVITIES

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CAMBRIDGE
AT THE UNIVERSITY PRESS
1945

PRINTED IN GREAT BRITAIN

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ACKNOWLEDGMENTS

The author wishes to make acknowledgment as follows for permission to reproduce various illustrations: 1 and 23, Cambridge University Press; 4, The Macmillan Company of New York; 6, The Zoological Society of London; 7, Houghton Mifflin, Boston; 10, The Royal Society of Medicine; 11, Sidgwick and Jackson; 14, The Wistar Institute of Anatomy and Biology, Philadelphia; 8, 15, 16, 17, Columbia University Press; 18, Dr E. J. Salisbury and George Bell and Sons; 19, 20, 21, 22, The Clarendon Press. Exact references to the sources from which the illustrations are taken will be found at the end of each chapter.

P R E F A C E

This book is an experiment or adventure in biological thought. I have tried to work out the consequences of rejecting the mechanistic point of view in biology, and I have, not unnaturally, arrived at a conception of the living organism and a method for biology which are entirely heterodox, and run counter to the ideas commonly accepted in the present theory and practice of biology.

My rejection of mechanism is quite deliberate and for good cause. The living thing *can* be treated as a physico-chemical system or mechanism of great complexity, and no one would dream of denying the validity and value of biochemical and biophysical research. But such an approach leaves out of account all that is distinctive of life, the directiveness, orderliness and creativeness of organic activities, and completely disregards its psychological aspect. I try to show that we cannot disregard these unique characteristics of life without losing all hope of building up a unified, coherent and independent biology.

I have kept clear of philosophical problems so far as possible, and based my case on recorded facts drawn from a wide field, but relating chiefly to animals.

E. S. R.

November 1943

THE DIRECTIVENESS OF ORGANIC
ACTIVITIES

1. I do not propose to revive the dead controversy between the mechanistic and the vitalistic theories of the living organism. Neither point of view is satisfactory, and neither is of much theoretical importance at the present day, though the mechanistic habit of thought is still persistent in most fields of biological research. Some quite different point of view is required.

It should be obvious that the analogy of an organism with a machine is superficial and remote, if only for the reason that the organism is a self-maintaining, reproducing and developing unity, and no machine is, or can be, that. But the mechanistic conception is one to which the human mind is peculiarly prone. Bergson was not far wrong when he said that the primary function of the intelligence was to think and deal with matter. *Homo faber* is in fact a more apt description of man than *Homo sapiens*, for wise he is not, as his regrettable history shows. His technology is superb, because he is by nature a mechanist. He has achieved amazing success in the mastery of his material environment by applying the mechanistic methods of thought and practice that come so naturally to him; what wonder then that he should apply the same methods to living organisms and think of them in the same way? And this conception of organism, quite inadequate as it is, has the great advantage of making unlimited research both possible and easy to the biologist, for the methods of

physics and chemistry are highly developed and ready to his hand, providing him with a superb technique and sparing him the heavy labour of thought about biological principles.

But it is quite unnecessary for the biologist to accept, even as a working hypothesis or guide to research, either materialism, or mechanism, or vitalism. Nothing compels him to do so. If he feels convinced that only by accepting mechanistic principles can he build up a truly scientific biology, he shows that he is still consciously or unconsciously dominated by the materialistic philosophy of nineteenth-century science, and by the natural human bias towards mechanistic explanations. As a philosophy, materialism is merely absurd; why then base biology upon it?

Many biologists, though they may not be at all convinced of the ultimate validity of the mechanistic hypothesis, yet find it convenient, even indispensable, in practice, and it determines and restricts the nature of their research. This is noticeable in much of modern work, especially in experimental biology. There is a concentration on what can be expressed in physico-chemical terms—elaborate and exact analysis of the physico-chemical environment, of the influence of external controlling stimuli on behaviour, of chemical factors in nutrition and reproduction, of the details of physiological functioning and their mechanism of action, of the presumed action of genes on development, and so on. The method of approach is analytical and disintegrative; there is little effort made to see the details in their biological relation to the whole organism; there is little attempt to tackle the fundamental problems presented by the organism as a living, developing, reproducing whole. Associated with this mental attitude is a firm resolve to have nothing to do with 'anthropomorphism' or with

'teleology'—in part quite rightly. With the natural human bias towards a mechanistic explanation, there goes an inability to see any alternative method of approach, save that of dualistic vitalism, which is rightly rejected. But actually, if one can rid one's mind of the bias to mechanism—which is by no means easy, as I, having struggled out of it, know to my cost—the real alternative method for biology appears simple and obvious. It is to regard living things and their activities so far as possible without preconceptions or unconscious bias, to investigate and study these activities as they appear to us in perception, accepting them, at least provisionally, as irreducible to activities of lower order. Methodologically, this is the obvious course for biology to adopt, and it is the only way in which it can free itself from the limitations imposed by the materialistic and mechanistic hypotheses. The central concept of a free biology must be living organism, not mechanism.

2. Now if we look at the facts quite objectively, putting firmly out of our minds the mechanistic preconception, we find clearly exhibited in the living organism a mode of activity which is shared by no inorganic object or unit and by no machine, namely, action directed towards end-states or goals which are normally related to the biological ends of self-maintenance, development or reproduction. This we may call directive activity. It can rarely be called purposive activity, for the organic agent concerned is seldom explicitly aware of the goal towards which its action is directed, much less of the biological end which it subserves.

At the risk of being labelled a teleologist, I maintain that biology must recognise and accept directive activity as an 'irreducible characteristic'* of life, and make a steady effort to establish the laws of this mode of activity. The

* See Broad (1925).

causal-analytical method which biology has taken over from the physical sciences is quite inadequate to its task; it yields a wealth of facts, and is a method of great practical value; it gives us much information about, but little understanding or comprehension of, living things and their activities. For such understanding we require a free biology, with laws and concepts of its own, independent of those of the physical sciences, based upon an objective study of the directive activities of organic agents, unrestricted by the hampering mechanistic hypothesis which is at the back of the causal-analytical method.

I adopt this point of view because, to put the matter crudely, it seems the only way to make sense of organic activities. To treat them as purely physico-chemical, to seek always for a causal-analytical explanation, and to analyse them without end,* is to get bogged in a vast intricacy of unrelated detail, and to lose sight of the biological significance of these activities, their active relation to the life of the organism as a self-maintaining, reproducing and developing whole.

That is what is happening in many fields of biology to-day. As a result mainly of mechanistic habits of thought and methods of research, directed towards a causal-analytical treatment of organic activities, we have now an enormous and bewildering accumulation of facts, segregated in separate and unrelated fields, a number of partial and unsatisfactory theories, often inconsistent with one another and none commanding universal assent, but no comprehensive and integrative view of the living organism, no biology as one coherent science.

Basic to the free biology which we require is the acceptance of directiveness as an irreducible characteristic of

* 'Analysis opens a vista of further analysis required... To arrive at one goal is to start for others' (Sherrington, 1922, p. 4).

life, explicable neither in terms of mechanism nor in terms of conscious purpose. It is a characteristic which most biologists refuse to acknowledge, being dominated still, to a greater extent than they realise, by mechanistic habits of thought, and fearing any concept that smacks of teleology. But we cannot leave out directiveness, or relegate it to metaphysics, as Claude Bernard advised, without abandoning all hope of understanding living things. And, as we shall see, acceptance of it does not commit us to teleology, in the ordinary sense of the word, and certainly not to dualistic vitalism.

The concept of directiveness was briefly developed in an address to the Zoology Section of the British Association some years ago (Russell, 1934), from which I may be permitted to quote the following passages:

‘Let us first try to rid our minds of the abstract notions of matter and mind, and regard the activities of living things without metaphysical preconceptions.... Taking this simple and direct view of living things, abandoning theory and accepting the obvious facts at their face value, we see first of all that the complete phenomena of life are shown only by individuals or organised unities.... There is accordingly no such thing as “living matter”, save as part of an organised unity. The second thing we note is that all living things pass through a cycle of activity, which normally comprises development, reproduction, and senescent processes leading to death. This life-cycle is in each species a definite one, passing through a clearly defined trajectory, admitting of little deviation from normality; it takes place generally in an external environment which must be normal for the species, and as a rule the internal environment also is kept constant round a particular norm. The activities whereby the needs of the organism are satisfied and a normal relation to the external

and the internal environment is maintained, may be called the maintenance activities of the organism, and they underlie and support the other master-functions of development and reproduction.

‘Our general definition or concept of organism is then an organised unity showing the activities of maintenance, development and reproduction, bound up in one continuous life-cycle. A static concept is inadequate; time must enter into the definition; the organism is essentially a spatio-temporal process, a “dynamic pattern in time”, as Coghill aptly calls it. Now all these activities are, objectively considered, directed towards an end, which is the completion of the normal life-cycle. One is tempted to use the word “purposive” in description of these activities, but this term is used in many senses and has a strong psychological flavour about it, so I shall use instead the neutral word *directive*, which I borrow from Myers (1932). It is quite immaterial from our simple objective point of view whether these directive activities, or any of them, are consciously purposive. The directiveness of vital processes is shown equally well in the development of the embryo as in our own conscious behaviour. It is this directive activity shown by individual organisms that distinguishes living things from inanimate objects’ (pp. 88–9).

It is true, I continued, that organised units are found also in the inorganic realm; a molecule is an organised system, and so also is an atom; in a certain very general sense they might be called ‘organisms’, or systems showing ‘wholeness’, as the supporters of ‘holism’ maintain. ‘But the living organism has characteristics which are lacking in inorganic systems, and it can be adequately defined or characterised only by reference to those peculiarities which we have just considered—the weaving together in one cyclical process of the master functions of maintenance,

development and reproduction. These distinguish it from any inorganic object or construction, from any inorganic system. Underlying these characteristics is the general directiveness of its activities, their constant drive towards a normal and specific end or completion' (p. 90).

3. That inorganic systems also may tend towards a natural end-state or terminus of action, by a process of 'closure', and are in this very general sense directed towards an end, is, of course, undeniable. But such end-state is a stable one of equilibrium or least action, whereas in the living thing the end-state or goal of the directive activities of development is a highly complex and unstable organisation, which can be maintained and kept in being only by constant activity of an elaborate and co-ordinated kind. And the more complex the organism the more unstable it is, the more in need of constant directive activities to keep it alive and functioning. 'When we consider', writes Cannon, 'the extreme instability of our bodily structure, its readiness for disturbance by the slightest application of external forces and the rapid onset of its decomposition as soon as favouring circumstances are withdrawn, its persistence through many decades seems almost miraculous. The wonder increases when we realize that the system is open, engaging in free exchange with the outer world, and that the structure itself is not permanent but is being continuously broken down by the wear and tear of action, and as continuously built up again by processes of repair' (1932, p. 20).

The unstable and self-regulating organisation reached in the development of a living organism is therefore something totally different from the stable equilibrium which is the natural end-state of an inorganic system. Life is a dangerous adventure; inorganic processes tend towards stability. It seems indeed fantastically improbable that the

complex and self-maintaining organisation of even the simplest living things can be built up by the free play of inorganic forces as we conceive them; there must be in life some different principle at work, even though we can form no adequate concept of what it is.

We should think then of the living organism, not merely as a unitary or holistic system, but as a unified complex of activities that are directive towards the completion of its life-cycle. They are also constructive or creative, for the organism does actually build up by its own powers, and in this sense create, its own elaborate structure in development and in the preparations for reproduction. There is in the life-cycle, which is the organism, no passive lapse into a static equilibrium, as in an inorganic system, but an active movement or drive towards the creation, maintenance and reproduction of a highly complex and specific functional organisation.

4. I propose in this book to test the value of what may, rather inaccurately, be termed a 'teleological' approach to the problems of life, based upon the acceptance of directiveness as an irreducible characteristic of all organic activity. Instead of ignoring the objective 'purposiveness' of vital activities, and assuming that somehow it can be accounted for by mechanistic processes of evolution, I shall put it in the forefront. I shall use, with due caution, and without any implication of conscious purpose on the part of the organism or other organic agent, the concepts of goal or completion and of biological end.

If we disregard ends and the directiveness of activities towards ends, we leave out what is distinctive in life, and we simply amass more and more data about the details of organic activities and the physico-chemical conditions of life, without connecting them up in a rational way with the functional life-cycle of the organism. This is what

J. S. Haldane meant when he wrote: 'When we endeavour to treat physiological phenomena as separable events we only reach unintelligible chaos to which there is no end. When we seek to understand them as manifestations of life regarded as a whole we find that we can make them intelligible and predictable' (1931, p. 76). They become intelligible, that is to say, when they are linked up with one of the main biological ends which the organism blindly pursues. 'Thus crude physical and chemical data relating to breathing or circulation can only become physiologically significant through proof of the part which they take in the co-ordinated maintenance of life' (p. 84).

If then it is true, and indeed the chief truth, about the living organism that its activities and those of its parts are directive towards living, reproducing and developing, we must, in our study of these activities, consider first and above all their biological significance or *function*, their relation to one or other of these biological ends. If we do not do so, but consider them separately, without relation to the life of the organism as a living, developing, reproducing whole, we shall never understand them, even though we succeed in working out their physico-chemical 'mechanism' or mode of action. We shall acquire, and go on acquiring, a vast mass of unrelated facts of biochemistry and biophysics, but we shall never build up a real biology. It is necessary always to think of organic activities in terms of their function, their relatedness to biological ends. That is a cardinal principle of the 'functional' biology whose laws and concepts I shall attempt to indicate. It is a principle which is in fact accepted, consciously or unconsciously, by many working biologists, who find that they cannot get on without such concepts as functional significance, need, norm, adaptedness and adaptability.

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EXAMPLES OF DIRECTIVE ACTIVITY IN THE MAINTENANCE AND RESTORA- TION OF STRUCTURAL AND FUNCTIONAL NORMS

In this and the subsequent section I shall try to illustrate the directiveness of organic activities, as shown in the maintenance and restoration of structuro-functional norms, and in the satisfaction of metabolic needs. This will give us a preliminary orientation in the use of the functional method, and pave the way for a fuller consideration of the goal-directed activities of living things. It is clear that a fundamental condition of active life is the maintenance of structuro-functional integrity, or wholeness, in such degree that the activities essential to life can be carried on in a co-ordinated and integrated way. This does not necessarily imply complete perfection of organisation, or absolute normality, but sufficient normality of organisation to ensure the performance of essential functions. It implies also the maintenance of sufficiently normal functional relations with environment to enable essential needs and requirements to be met. Leaving over the question as to how a normal functional organisation is built up in the course of development and normal relations with environment established, we shall consider in a few selected examples how these norms are actively maintained—for they are nothing static or fixed—and in particular how they are restored, if disturbed, or adapted to new conditions that may arise; and we shall regard these maintaining and

restoring activities, which may be physiological or morphogenetic or behavioural, in their proper light as directive towards goals related to the general biological end of survival. Let me say again that this way of looking at biological activities in no way implies that they are consciously purposive; we have every reason to think that they are not, or only rarely so. Nor should we think of survival as being consciously an end or purpose for the animal itself. That is why I call it a biological end.

1. THE HEALING OF WOUNDS

The closing up and healing of superficial wounds is a phenomenon of great interest and biological significance, and an admirable starting point for its study is provided by Wigglesworth's paper (1937) on the healing of small wounds and burns in the hemipteran *Rhodnius prolixus*, where the essential processes involved are seen in their simplest form. Beneath the cuticle of this insect there is a single layer of epidermal cells upon a basement membrane; if an incision is made in this, or a small area excised, the following responses occur. The cells in the neighbourhood become activated and migrate towards the edges of the cut (Fig. 1, *cz*); haematocytes accumulate in the same area beneath the basement membrane. The epidermal cells that have congregated at the site of injury then spread over the excised area (*sc*); in simple cases, where the wound is small and the basement membrane intact, 'the wound is quickly covered by a few cells spread excessively thinly but still connected by their cytoplasmic processes. As more cells follow these the nuclei become more and more crowded until the normal density is reached; spreading then ceases' (p. 367). Cell division occurs after migration, and takes place mainly in the

peripheral zone (sz) where cells have become sparse owing to migration towards the cut.

Temporary repair of the cuticle itself is effected by the drying of the exuded blood, which slowly forms a plug of cuticulin; later on, new cuticle is formed over the wound. The epidermal cells that migrate towards the cut and spread over it form at first a layer several cells thick, but the normal structure of a one-layered epidermis with cuticle above and basement membrane below is slowly restored, by the degeneration of the unwanted cells in the lower layers, and by the secretion of cuticle and the formation of the basement membrane by the remaining epidermal cells. Finally, any overcrowding of cells round the margins of the wound, which may have resulted from the initial process of migration, is relieved and normal density restored by the degeneration of superfluous cells.

By appropriate technique it is possible to destroy a

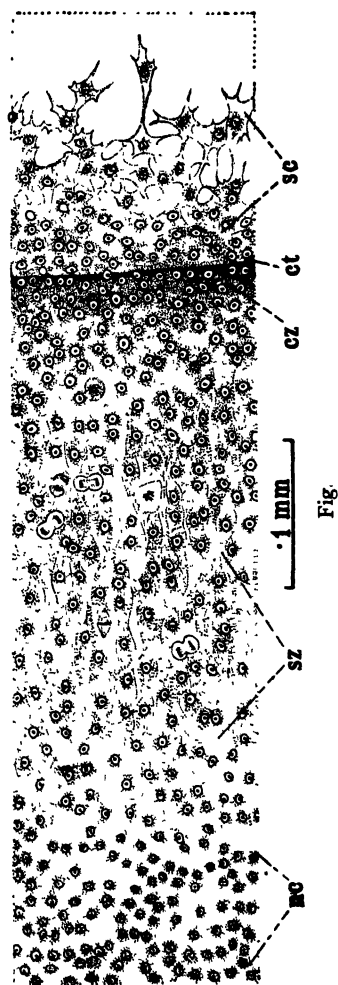


Fig.

group of epidermal cells by heat without injuring the cuticle. The healing of these burns shows significant differences from the healing of cuts. There is little migration towards the margin of the burn; spreading takes place usually between the burned cells and the cuticle, and multiplication of cells takes place in the zone of spreading, and not in the peripheral zone outside the zone of migration, as is the case with incised wounds.

What now are the factors initiating the process of wound-healing in *Rhodnius*? Observation shows that the migrating cells are specially attracted towards areas containing dead and damaged cells, and this suggests that the stimulus to activation is provided by chemical substances produced by the injured cells, and that migration towards the wound is a 'chemotactic' response to these substances. But perhaps the interruption of continuity in the epidermal cells (which form a syncytium) is also a factor? By a number of ingenious experiments Wigglesworth has shown that activation and migration can be induced where there is no break in the epidermis; hence the chemical factors by themselves can induce the initial responses in the healing process.

As to the nature of these chemical factors, Wigglesworth adduces evidence that a considerable range of substances will stimulate activation and migration, but they have the common character of being protein-degradation products, such as are produced normally in the autolysis of dead and dying cells.

The cause of the spreading of epidermal cells over the wound is not known; it is an example of 'thigmotaxis' in that the cells apply themselves closely to flat surfaces, but this does not seem to be a sufficient explanation of the active spreading. It is much more likely that 'the lack of continuity in the epidermis must be responsible for the

continuance of growth. Growth (cell movement and cell division) does not cease until this continuity has been restored and a normal density of normal nuclei has been established' (p. 378). As Wigglesworth rightly points out, there are here involved 'regulative' factors which are not to be explained in terms of simple chemotactic and thigmotactic responses.

His summing up of the process is significant and important. 'Products of the partial autolysis of proteins in the damaged cells activate the surrounding cells and provide the chemotactic stimulus to migration. They do not evoke cell division unless the mutual relation of the cells (the sparseness of their nuclei) demands an increase in their number. Growth ceases when the products of autolysis have been removed and the epidermal cells have recovered their equilibrium by spreading over the wound, by mitosis in the sparse zones, by degeneration in the dense' (p. 379).

The whole process is a directive one, aimed at the restoration of the structural and functional normal state. I use the word 'aimed' advisedly, but without any implication of conscious purposiveness. The end-state or terminus towards which the process moves is the restoration of the continuity of the epidermis, the replacement of cuticle and basement membrane, the re-establishment of the normal density of nuclei—a complex result, reached through appropriate activities of cells, which are here the agents concerned. These activities are of several kinds. They are behavioural—as shown in the active migration and spreading of the epidermal cells. They are physiological, as in the secretion of new cuticle. They are 'morphoplastic',* as in activation and cell division; cells also degenerate where they are superfluous or unwanted.

* A word I proposed in my *Study of Living Things* (1924, p. 85).

The nature of the stimulus that excites the preliminary stages of the healing process—activation and migration—is of great interest. In normal conditions, an inevitable concomitant of injury is the damaging and destruction of cells, followed by autolysis and the liberation of protein-degradation products; it is these that form the effective or valent stimulus. Normally, the occurrence of these substances is associated with injury and the need for repair. They are, therefore, *normally adequate signs* of the need for restorative action. In unusual conditions, induced by experiment, the valent stimulus may occur in the absence of its usual cause, injury to the epidermis, and it is followed by the initial responses of wound-healing, though there is no wound to be healed. Thus the stimulus, which is normally adequate as an indicator of injury, is here 'misleading'. We shall see later that in instinctive behaviour also the valent stimulus or percept is normally adequate; in unusual relations, however, it may induce biologically inadequate behaviour, as in many cases of the so-called aberration of instinct (see Russell, 1941).

We may note also that it is not one specific substance that evokes response; there is a range of valent stimuli.

The results obtained by Wigglesworth as to the nature of the 'formative stimulus' in wound healing confirm those arrived at by Carrel (1930) in his studies of the process in mammals, especially dogs. In Carrel's view the essential role in the initiation of wound healing is played by the split proteins liberated by the damaged cells, aided in some cases by the polypeptides manufactured by the leucocytic ferments from cell debris and coagulated fibrin lying on the surface of the wound. Thus, 'the traumatism determines directly or indirectly the production by the tissues themselves of the formative stimulus'. Also the 'wound hor-

mones' in plants, which stimulate repair, appear to be products of autolysis of the injured cells.

As regards the covering over of the wound, it is clear from Arey's review of the evidence (1936) that in the higher vertebrates this takes place mainly by migration of epithelial cells, as in *Rhodnius*, preceded in large wounds by an active contraction of the tissues round the wound, so that the area to be repaired is reduced. The chief factor in the covering over, or epithelisation, of the wound 'is cell movement, apparently by amoebism. Mitosis is not a feature of the initial stages and in small wounds may not show any increase until after the epithelisation is complete. In such cases the mitotic region may be quite outside the repair area, and this activity can then be interpreted as compensatory and for the purpose of restoring cells lost to the wound by emigration... In wounds so large that the adjoining epithelium cannot supply sufficient cells within a comparatively short time, cellular proliferation then enters before epithelisation is complete, and cell movement and proliferation go on simultaneously' (pp. 351-2). All goes on then as if the aim were to restore the normal density of cells by two methods, migration and proliferation, which are complementary.

Arey also considers the problem of what induces the cells to migrate out across the wound. Stereotropism or thigmotaxis explains why the cells keep to the floor of the wound or along the fibres in the coagulum, but 'there is apparently another agency at work which directs the cells away from their own tissue into the neighbouring foreign material and especially into the wound defect' (p. 395). Arey points out that at their free margin the cells are exposed to a foreign environment which sets up differences of electrical potential and surface tension. It is these differences, he thinks, that induce a movement in the

direction of the wound. This seems a somewhat hypothetical interpretation, and it seems more likely that, as Wigglesworth points out, the actual lack of continuity is itself the stimulus to migration. The view is expressed by Fischer (1930) that this stage of repair is initiated by a disturbance of the normal equilibrium of the cells, such as is caused 'through the want of neighbouring cells, at the margin of a cell colony or at the margin of a cut'.

To sum up—the stimulus which initiates the process of wound healing is a class or range of substances normally formed as a result of injury to the epidermal cells. These substances are *normally adequate signs* of injury and the need for repair. The spreading of cells over the wound is elicited by lack of continuity experienced by the cells at the margin of the wound. The process as a whole moves, or is directive, towards the restoration of the normal functional structure, towards this particular end-state or terminus of action. The restoration of the normal density of cells is achieved by migration, by multiplication of cells, and by the degeneration of unwanted cells, all of which processes are aimed at restoring the norm.

It seems impossible even to describe these events accurately without using terms and concepts such as norm, need, adequate stimulus, reception-disposition to respond to such stimulus, and activity directive towards the attainment of a normal end-state or goal.

2. REPAIR THROUGH BEHAVIOUR

Let us take now an example of a very different kind, illustrating the restoration of structuro-functional norms through the behaviour of the animal as a whole, not through the co-ordinated activity of its cells.

The caddis larva *Molanna*, the behaviour of which has been studied with great care by Dembowski (1933), builds

for itself a case of characteristic shape and structure which is normal for it. The case is usually made of sand grains, though other materials may be used, and it consists of a conical tube widening towards the mouth, provided on either side with a flange or wing which projects considerably over the mouth.

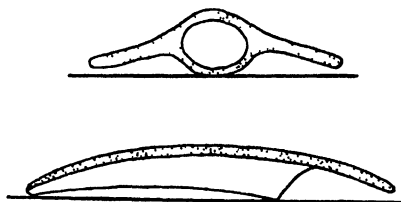


Fig. 2

If the larva is deprived of its case, it will proceed to construct a new one of the normal pattern. It buries itself in the sand, back downwards, and pushes a mass of sand grains towards its head, where it binds them into a loose bundle with silk produced from the labial glands. This forms a sort of anchor or holdfast to which the larva clings by its anal hooks while it gets on with the job of making a case. It makes first a ring or section of tube round its body, searching about for material, picking it up and often rejecting what is unsuitable, fitting suitable pieces accurately into the growing mosaic and binding them with silk. By addition of material to its anterior edge the ring is gradually extended into a tube, and when it is long enough the larva cuts it free from the holdfast. It builds the wings by stretching at full length out of the tube, but as it always keeps its anal hooks inside the tube it cannot reach back far enough to complete the hinder part of the wings. It usually achieves the normal and typical shape by lengthening the tube in front and cutting it off behind.

Cutting away of an unwanted part may also occur in the following circumstances. A number of larvae are ejected from their cases, but given an opportunity to return to them; they do not sort out accurately each into its own case, and it happens that a small larva acquires a large case; next morning it is found to have cut a piece off the front end of the tube (Fig 3, *a*), and next day a large part of the overhanging roof (*b*), thus adjusting the size of the case to its own requirements.

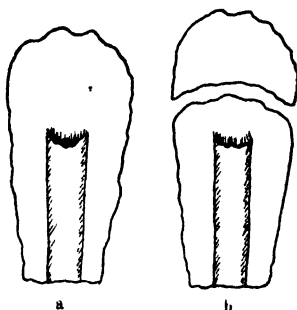


Fig. 3

If constrained to build with insufficient material, the larva may utilise for construction material taken from the holdfast, using this up completely; material is used in accordance with the dominant need or drive, which is to build the case.

Dembowski carried out a large number of experiments on the repair of the case with interesting results. If the roof or part of it is removed, or if the roof is damaged, the missing parts are completely restored. Here reconstruction is simply a repetition of original construction, and a straightforward replacement of missing parts. If, however, the hind part of the case (up to 15 % of its length) is removed, the larva does not replace it, but builds on to the

case in front, sometimes too little, sometimes far too much. If the posterior half of the case is cut away, it generally extends the case in front to more or less normal proportions; but it may reverse its direction in the tube, restore the missing part, and then turn back to the front end. In five cases out of the thirty-two studied, the larva permanently reversed its direction, building a tube with wings and roof at the hinder end and making that functionally the front end. In one case the larva made a roof at the hind end, then cut it off, turned back and extended the case in front.

If two-thirds of the case are removed from behind, the response is extraordinarily variable. Of fifty-four cases no two were restored in exactly the same way, but six main kinds of response may be distinguished. The larva may (1) build a complete new case, using the old piece simply as a holdfast and later cutting it off, (2) restore normality by building on in front, (3) build on at the hind end, then turn, cut off roof and part of tube, but rebuild them, (4) build a new front end on the hinder part and inhabit it, while the original front is left intact, (5) build a new front end behind and trim off the original front, so that the polarity of the case is completely reversed, (6) build first in front, then cut off the new roof, reverse and build at hind end. In twelve cases out of the fifty-four polarity was more or less completely reversed.

The stimulus to restoration is in all cases the tactile perception of something missing. 'The body of the larva is always in contact with the inside of the tube, and the animal can very well detect when anything is missing' (p. 296). The animal will live quite happily in a piece of hollow stem, which satisfies its contact needs, though it will build a roof to it and then extend the tube somewhat.

It will be seen that the varied behaviour of the *Molanna*

larva in response to damage to its case is directive towards the restoration of the normal state, and is elicited by lack of the normal contact relations. It is clear too that the same *functional* end-state, enabling normal life to continue, is reached by many different ways. Restoration of the normal structure of the case is not always achieved; the larva may be left with two front doors, as in the instances of 'polar heteromorphosis'; but often it will cut away what is unwanted, and achieve a good approach to structural normality.

It is noteworthy also that in responding to these operational defects the larva has to deal with unusual contingencies, which are unlikely to have presented themselves in its individual or its racial history; its power of effective response is therefore something fundamental and primordial, not to be accounted for by selection. Very often, an animal's instinctive response is limited and stereotyped, adequate to deal with the usual contingency and not very adaptable to the unusual (see Russell, 1944). The plastic behaviour of *Molanna* serves to remind us that the specialisation of instinctive behaviour is by no means absolute or universal; it is more probably a secondary development, a restriction or limitation of the general power of adaptive response which all organisms possess in greater or less degree.

As Dembowski very rightly points out, the processes of repair and reconstruction of the case, which the larva of *Molanna* effects through behaviour, show a striking similarity to the phenomena of regeneration and restitution, which are due to cell activities. Points of resemblance are as follows: (1) repair tends to take place in the direction of normal growth, as is shown especially in the replacement of anterior defects; (2) there may be, not a simple replacement, but a restitution of the case as a whole, when a

large part of the hind end is removed; (3) polar heteromorphosis is of frequent occurrence, and also hyper-regeneration; (4) the rate of restoration is proportional to the amount of damage; and (5) 'morphallaxis' (see p. 138) may occur. The last-named phenomenon is shown when, if the roof is removed and no loose material is available, the larva constructs the missing part with fragments taken from the case, and when the larva building a new case withdraws material from the holdfast if it can find none around it.

The analogy between simple repair and wound-healing will not have escaped the reader; there is the same response to something missing, the same directive action towards the restoration of normality, the same elimination of what is unwanted.

3. THE NEMATOCYSTS OF *MICROSTOMA*

A very remarkable case of the directive activities of cells and of the animal itself in establishing a structuro-functional norm is provided by the Rhabdocoele *Microstoma* (Kepner and Barker, 1924; Kepner, 1925). This little 'worm' is commonly found to be armed with a large number of nematocysts imbedded in its ectoderm, pointing outwards and ready for action. It does not produce these nematocysts itself, but obtains them from *Hydra*. Though *Hydra* is a dangerous animal for it to attack, and sometimes overpowers it, a *Microstoma* lacking its complement of nematocysts will fall upon a *Hydra*, paralysing a part of its body by means of a secretion thrown out from the mouth. It then ingests the *Hydra* in whole or in part, and digests all but the nematocysts, which remain lying free in the enteron. Later the nematocysts are taken up by single endodermal cells, arranged with the blunt end towards the base of the cell, and pushed through into the mesoderm. 'Eventually

about each nematocyst a wandering mesodermal cell will crowd. This mesodermal cell ingests the foreign nematocyst and then transports it to the ectoderm of *Microstoma*. At this phase of the process as many cells are involved as there are nematocysts, each transporting a nematocyst. These cells, acting independently, carry their respective nematocysts to the surface of *Microstoma* in such manner that the *Microstoma* comes to have nematocysts at its surface *uniformly distributed* and all properly oriented. Here the attending cells retain them indefinitely' (Kepner, p. 66). Many of the stages of this process are shown in Fig. 4. The normal end-state or terminus of this directive action by the endodermal and mesodermal cells of *Microstoma* is then a sufficient number of nematocysts equally spaced out—a normal density of nematocysts, in other words.

Experiments by Kepner and Barker have shown that *Microstoma* eats *Hydra* for the sake of its nematocysts rather than for its food value. Specimens containing few or no nematocysts attack *Hydra* readily; those with many or a full quota of nematocysts refuse *Hydra* for some days, even when hungry. One 'fully loaded' *Microstoma* which had been starved until it would accept *Hydra* digested the flesh of the *Hydra*, but rejected the nematocysts through its mouth. Conversely, a recently fed *Microstoma* with few nematocysts may reject the flesh of a *Hydra* it has eaten and retain the nematocysts. It appears therefore that need for the full complement of nematocysts is the main controlling factor inducing *Microstoma* to attack *Hydra*. Hunger may also induce *Microstoma* to attack, but if it has already its full quota of nematocysts it will take up no more.

The aim of the actions by *Microstoma* and its cells is then to establish a normal distribution of nematocysts over its surface, just as the normal density of the epidermal cells

in *Rhodnius* is restored after injury, by spreading, cell division and the degeneration of unwanted cells.

It is clear that for the interpretation and understanding of these remarkable facts we require the concepts of need,

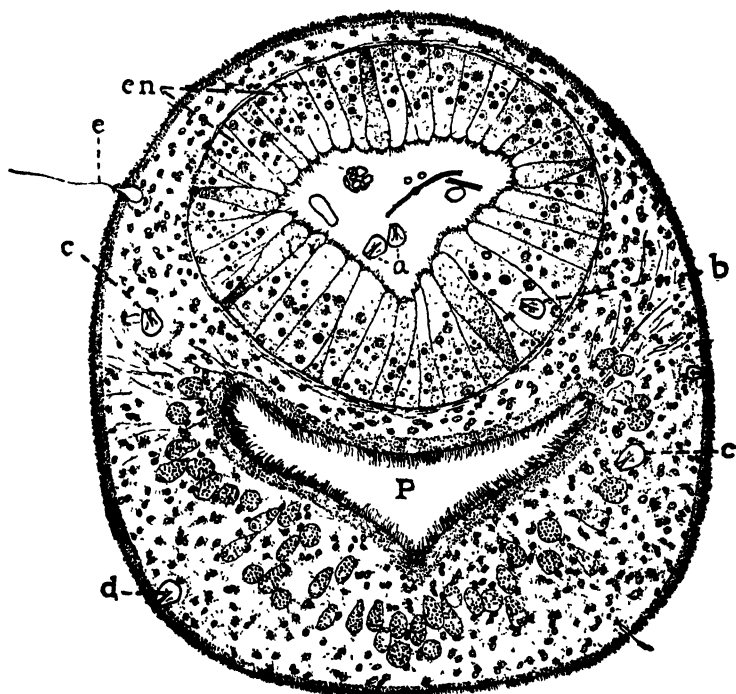


Fig. 4

normal end-state or goal, and directive activity towards attainment of goal. Later work by Kepner and his collaborators (1938) adds some interesting refinements to the story. They studied the behaviour of the cells of *Microstoma* (or *Microstomum*) towards the nematocysts of

the green hydra (*Chlorohydra viridissima*), using specimens of *Microstoma* belonging to a clone that had not been in contact with any hydra for forty-nine generations. There are four different kinds of nematocyst in this green *Hydra*, known as penetrants, streptolines, stereolines (or glutinants) and volvents. The first is a large nematocyst with a barbed thread which is discharged into the body of the victim; the streptoline is smaller and simpler, but has also a penetrating thread. The other two have adhesive and prehensile threads respectively, which do not penetrate, but serve to hold the prey. All four kinds are found in batteries on the tentacles of the *Hydra*, the penetrating kinds also on the peristome and body, from which, however, the adhesive kinds are missing. Now when *Microstoma* ingests these different kinds of nematocyst, they are all transported as far as the mesoderm or parenchyma, in the manner described above, but only the penetrants and the streptolines are taken into the epidermis. 'The stereolines and volvents, which if carried to the epidermis to function there would hinder the microstomum rather than aid it, are taken up by the parenchyma and digested' (p. 118). A hundred hours after ingesting the *Hydra*, *Microstoma* shows orientated stinging nematocysts in the epidermis and none of any kind in the parenchyma. The epidermis is deeply pitted both externally and internally just above the orientated nematocysts, but is not ruptured until the nematocyst is discharged. As Kepner points out, the fate of the nematocysts depends upon the need or 'demand' that *Microstoma* has for them. 'An animal that lacks tentacles has no demand for either glutinants or volvents. Hence, when glutinants and volvents are delivered to the parenchyma they are digested by phagocytic parenchyma cells. The penetrants and streptolines, on the other hand, are transported to and oriented at the epidermis. But even

these, if there be a full complement of them at the epidermis, are rejected by the endoderm and thrown out at the mouth of the worm. A "loaded" microstomum has no demand for even penetrants and streptolines, so they are rejected also. Here again the fate of nematocysts depends upon the demand for them' (p. 120).

4. REGULATION OF THE NUMBER OF ERYTHROCYTES IN MAMMALIAN BLOOD

The blood of a healthy man, living in an atmosphere of normal barometric pressure and oxygen content, contains about five million erythrocytes per cubic millimetre. This appears to be the appropriate concentration which enables adequate oxygenation of the tissues to take place, while avoiding undue viscosity, which would slow down circulation. It is, in normal circumstances, the right or normal concentration. But it is an adjustable or adaptable norm; it can be increased according to need, by the active production of new erythrocytes from the red bone-marrow, and it can be reduced, if it is excessive, by the active destruction of superfluous erythrocytes by the macrophages of the lymphatic glands. The conditions under which either increase or reduction of the mass of red corpuscles takes place have been summarised by Boycott (1929) in a remarkable paper, in which he points out the great practical value of a 'teleological' approach to the problems of pathology and of biology in general. Though for details of the complex physiological activities concerned reference must be made to Boycott's paper and the literature cited therein, I shall endeavour to give the main facts as simply and accurately as possible. They are of great interest as bearing on the relation between biological norms and biological needs, and illustrate very nicely the directiveness of cellular activities.

An increase in the number of erythrocytes, or, as Boycott calls it, a hypertrophy of the erythron, 'has only one known cause—a deficient oxygen supply to the tissues. This may be brought about in a variety of ways. The best known is the polycythaemia, due to living at high altitudes, which, as the Pike's Peak expedition showed, is a real increase in the red corpuscles and not a concentration of the blood from loss of plasma. The same result has been obtained many times in experimental animals, by exposing them either to rarefied air or to gas mixtures deficient in oxygen at atmospheric pressure' (p. 2). A difficulty in breathing, such as is caused by an obstruction in the trachea, and certain defects in the heart which slow down the circulation, will also bring about an increase in the number of erythrocytes, and this may occur too in chronic carbon monoxide poisoning. The oxygen need of the tissues set up by these conditions is relieved or satisfied by the increase in the erythron, for 'a smaller proportion of the total amount of oxygen in the arterial blood is used up during its passage through the tissues; hence the oxygen pressure in the venous blood is maintained at a higher level, and any lowering of oxygen pressure in the tissues is diminished or avoided' (p. 3). The normal quantity of circulating red corpuscles is raised to meet the increased need of the tissues for oxygen. The agents that are active in producing this increase are the cells in the red marrow that give rise to the erythroblasts or young nucleated red corpuscles.

Perhaps more remarkable is the fact that the number of erythrocytes in circulation may be greatly reduced if the oxygen supply is excessive. This takes place in animals kept in compressed air, or in air enriched with oxygen at atmospheric pressure; experiments with rabbits have shown that when they are kept in air containing two to three times the normal amount of oxygen the erythron may be

reduced by as much as one-third. The inverse relation between percentage of atmospheric oxygen and number of erythrocytes is illustrated in the following table, relating to a rabbit investigated by J. A. Campbell:

Oxygen % in air breathed	Red cells millions (in cu. mm.)
7	9.5
9	9.0
11	7.5
19	5.5
55	3.0

A direct reduction in the size of the erythron can be brought about by bleeding, and an increase by transfusion, and it is interesting to see that in both cases the normal size is rapidly and actively restored. The body has two ways of dealing with the loss of red corpuscles through haemorrhage. The spleen, as Barcroft has shown, is a reservoir of these corpuscles, which are there highly concentrated. When severe haemorrhage occurs, the loss of corpuscles is first made good by contraction of the spleen, which squeezes out its store into the circulation. There occurs later an increased manufacture of erythrocytes in the marrow to make up any remaining deficiency. It is a curious point that with successive bleedings the rate of replacement increases; practice improves performance.

The erythron can be increased in size by transfusing an extra quantity of blood into the circulation; when the extra plasma has been got rid of, there is a polycythaemia comparable to that produced by life at high altitudes. But the body does not need the extra cells and it proceeds to dispose of the excess, not by letting them die off as they become worn out, but by an active process of destruction by phagocytosis, which process also can be accelerated by

practice. What the stimulus is that leads to destruction of the excess cells is not known, but it is probably not the increased viscosity consequent on the polycythaemia.

The general conclusion to which Boycott comes is that 'hypertrophy' and 'atrophy' of the erythron are both determined by the needs of the body, that 'the erythron is reduced in size by so much of it as is unnecessary, and increased in size by so much of it as is found requisite to relieve the anoxaemia of the tissues'. He makes the pregnant suggestion that hypertrophy and atrophy generally may not be due to simple use and disuse but may be essentially determined by the needs of the body.

5. HYPERTROPHY AND ATROPHY OF LIVER AND KIDNEYS

Evidence for the view that hypertrophy and atrophy are determined by need rather than by use and disuse is given by Boycott in the paper cited, and also in greater detail in a later publication (1932).

If half the liver is removed in such animals as dogs and rabbits, the remaining half will grow until the normal amount is restored, provided the liver is healthy. The enlargement takes place through the production of a greater mass of liver cells round the portal canals and not by the formation of new lobes; the lost lobes are not regenerated. But if the central parts of the lobes are destroyed by chloroform the loss will be quickly made good by regeneration. Hypertrophy and regeneration are therefore equivalent means of restoring the normal amount of liver tissue.

Hypertrophy is not the automatic result of amputation; it does not take place in a starving animal, in which little work is thrown on the liver.

That atrophy also is conditional, and not automatic, is shown by the classical experiment of Rous and Larimore, which is described by Boycott as follows: 'If the portal vein going to part of the rabbit's liver is tied, the liver tissue involved progressively atrophies to a fibrous tag, though it still receives blood through the hepatic artery which would be sufficient to keep it alive; simultaneously the normal part of the liver progressively hypertrophies in proportion as the rest atrophies. If, however, this adaptive growth is prevented by tying the bile ducts coming away from the part which should hypertrophy, the part with the tied portal vein does not atrophy. Tying the portal vein, therefore, "causes" atrophy only if the rabbit can provide an adequate amount of liver elsewhere; what happens is not irrevocably predestined by the operation' (1932, p. 10). It is *need* that determines whether or not the part shall atrophy.

If one kidney is removed or put out of action by ligature of the ureter, the other kidney shows a compensatory hypertrophy, under certain conditions. In the dog, hypertrophy of the remaining kidney does not occur, if the animal is kept on a bare maintenance diet; on the other hand, hypertrophy takes place more rapidly on an excessive proteid diet. Both kidneys, left intact, will increase in size if the animal is given a diet composed mainly of proteids.

As with the liver, atrophy also is conditioned by the needs of the body. Normally, ligature of one ureter is followed by progressive and complete atrophy of that kidney, with a corresponding hypertrophy of the other. When hypertrophy of the latter is under way, removal of the obstruction to the ureter of the operated kidney does not put a stop to its atrophy, which continues, though the kidney can now function. But if, when the obstruction is

relieved in the operated kidney, the other kidney is removed completely, the process of atrophy ceases and the operated kidney builds itself up anew. Here again, need determines whether atrophy continues or not. The stimulus leading to this regrowth and hypertrophy is not known, but it may be, as Boycott suggests, an excess of waste products in the blood.

It is to be noted that atrophy or reduction is not always a passive process due to cessation of functional activity. If an arm is cut off just above the elbow, the bones, muscles and nerves concerned in moving the forearm largely waste and disappear. But the mutilated humerus is reorganised into a smaller whole; the process of reduction is an active one. 'In other instances function is not prevented, it is merely not wanted, as in the overgrown capillaries of granulative tissue or in the blood-vessels of the parturient uterus. As the inflammation subsides, the excess of capillaries disappears, and after childbirth the uterine arteries are brought back to their resting calibre by making new arteries inside the old ones, another example of achieving atrophy by growth' (p. 3). What is not wanted is removed, and if necessary replaced on a smaller scale. Atrophy, therefore, though it may be due sometimes to disuse and functional inactivity, is best regarded, like hypertrophy, as 'an adaptive process, a process by which the body adjusts itself to changed conditions of life'

The conclusion appears justified that use and disuse are not the only 'causes' of hypertrophy and atrophy respectively, nor probably the real deciding factors; it is the need or want of the body as a whole that is decisive. What is needed will be supplied by hypertrophy, and what is not wanted will atrophy or be actively removed.

6. REGULATION OF BODY-TEMPERATURE NORMS

In considering the regulation of body temperature it is of course important to make a broad distinction between poikilothermic and homoiothermic animals. But it should be remembered that the distinction is not hard and fast. Poikilothermic animals have not always the temperature of their surroundings, and homoiothermic types do not all of them maintain a steady body temperature.

An active animal always produces some amount of heat; this gives rise in poikilotherms to a temporary rise of body temperature, which may be very considerable. Insects in flight, especially Hymenoptera and Lepidoptera, may have thoracic temperatures 10° C. or more in excess of the air temperature. Sphingids, according to Wigglesworth (1939, p. 359), 'are said to be unable to take flight until their body temperature has been raised to $32-36^{\circ}$ C. by preliminary fluttering, and during flight a temperature as high as 41.5° C. has been recorded in one insect'. So insects may temporarily become 'warm-blooded' (see also Krogh and Zeuthen, 1941; and Gunn, 1942, p. 303).

Some bats apparently are poikilothermic when at rest and imperfectly homoiothermic when in flight. When asleep they have a temperature closely approximating to that of the air and varying with it, but when they are aroused, or when they wake naturally at dusk, they undergo a rapid rise in temperature, produced mainly by shivering and a rhythmic flexing of the legs. The rate of warming up is considerable. Burbank and Young (1934), to whom these observations are due, found that a greater horseshoe bat warmed itself up from 20 to 39° C. in the course of half an hour. The bat is able to fly when it has reached a temperature of about 30° C. The maximum temperature reached varies to some extent with the

external temperature, but in the species studied, body temperature is mainly a function of activity. 'As soon as the movements of a bat decrease, its temperature begins to fall, and every change in activity is accompanied by corresponding fluctuations of temperature' (p. 462).

In the hibernation of bats and other small mammals it is well known that body temperature falls to very nearly the level of the air temperature and is sometimes as low as 2° C. (Johnson, 1931).

Young mammals and young birds regulate their temperature very imperfectly, and are usually dependent for body heat upon the warmth of their parents. Birds show considerable fluctuations in temperature (Kendeigh and Baldwin, 1928), and some, like the humming birds, may fall into a temporary state of 'torpidity' when their temperature falls (Huxley, Webb and Best, 1939).

Most adult mammals appear to be homoiothermic, maintaining a steady body temperature—except when they hibernate—whatever the temperature of their surroundings may be. Normal temperature means range from about 36 to 40° C. according to species (Wislocki, 1933), and temperature does not normally vary more than a degree or so round the mean. In monotremes, however, the normal temperature is distinctly lower, somewhere about 30° C., and it varies considerably according to external conditions—regulation of body temperature is imperfect. The same is true of sloths, and to some extent of armadillos and ant-eaters. The rat also shows a temperature variation of about 4° C. in an air-temperature range from 5 to 40° C.

The maintenance of a steady temperature in those mammals that keep their body heat constant depends upon a balance between heat production and heat loss. Heat is constantly being produced by the activities of organs, and especially by muscular action. The normal rate of pro-

duction is remarkably steady; the 'basal metabolic rate' is one of the constants of the organism. Heat is lost by radiation and conduction from the skin, by evaporation of sweat, and by the expulsion of heated air in respiration. Regulation of temperature can be achieved 'by increasing or decreasing the rate of heat loss or by increasing or decreasing the rate of its production, according to need' (Cannon, 1932, p. 182).

Let us consider first what happens when a warm-blooded mammal is exposed to temperatures considerably below the normal temperature of its body. A whole series of physiological responses come into play. Perspiration is reduced; the surface blood vessels are constricted; the coat is fluffed out. (We see the last remains of this coat reaction in the 'goose-flesh' produced by cold on the human skin.) These responses tend to prevent heat loss. Other reactions set in to increase heat production; more adrenal secretion is passed into the blood, producing an increased heart beat, and a higher rate of metabolism; shivering may take place, producing heat through involuntary muscular contractions. If the adrenals are put out of action, shivering occurs to a much greater extent. The centre through which these physiological responses work is situated in the diencephalon, and acts, to use Cannon's words, like a 'delicate thermostat'.

But this is by no means the whole story. In addition to its physiological responses the animal may, and often does, show behavioural responses. The chilly dog lies beside the fire or creeps into the sun; puppies huddle together for warmth; many animals seek shelter and curl themselves up to keep warm; some may migrate to warmer climates; others may hibernate. Man protects himself from cold by warm clothing and heated houses, and some migrate. In a highly civilised state man may even establish

a steady temperature in his immediate environment in his house, his office and his car, thus rendering physiological adjustment almost unnecessary.

As an example of behavioural response to cold, let us take the nest-building activity of rats, which has been carefully investigated by Kinder (1927), in Richter's laboratory in Baltimore. Nest-building in rats is an instinctive activity, arising as early as the 20th day. Young rats reared in sawdust—which gives no opportunity for nest-making—built perfect nests at 30 days old as soon as they were given strips of crêpe paper (Richter, 1927). Both males and females build nests throughout life, the males solely in response to temperature needs, the females mainly in relation to the need for warmth, but showing a marked increase in nest-building towards the end of pregnancy and during lactation, related partly to the needs of the young. In Miss Kinder's experiments the rats were given a supply of strips of soft paper; the nest was removed each day and the number of strips used were counted; the rats had thus to make a new nest every day. Her experiments demonstrated in a quantitative way that within normal temperature limits in the environment (50–80° F.) higher temperatures led to a decrease, lower temperatures to an increase in nest-building. Also the nests built in cold conditions were compact and closely constructed, those in warmer conditions loose and scattered. At temperatures above 80° F. nest-building ceases except by mothers suckling young. When running activity is high, resulting in production of heat, nest-building is low; when the need for food and warmth is great, as in prepubescence and starvation, nest-building is above average, as it is also in lactation. The thermoregulative function of nest-building is further shown by the fact that nests are invariably built in the corners or against the wall of the cage, out of draughts.

Removal of the hypophysis in rats produces, probably through the consequent reduction in the activity of the thyroid, a decrease in metabolism, a lowered temperature, reduced general activity and less interest in food (Richter and Eckert, 1936). It brings about, however, a very marked increase in nest-building activity, of the order of 178 % increase in the 10-20 day period after operation. It is noteworthy too that the nests made are more compact and closely woven. 'In contrast to the loose, shapeless nests of most normal animals, several of those built by hypophysectomised animals had the shape of a ball that looked like a large hornets' nest with a single small opening about $1\frac{1}{2}$ inches in diameter. The paper was woven so tightly that the nest could be lifted, intact, simply by hooking a finger into the entrance hole' (p. 566). This increased nest-building, Richter and Eckert concluded, must be regarded as an effort on the part of the animal to maintain normal temperature. 'The behaviour effort of the animal to conserve body heat is just as important a part of the heat-regulating mechanism as any of the simpler physical or chemical means, such as the metabolism of fats in cold temperatures' (p. 568).

Another behavioural response to cold is increased appetite and increased intake of food; more energy is required to keep up the normal temperature of the body, and this is supplied by eating more food. It is probably lack of food and of opportunities for obtaining food that forces many mammals and birds of high latitudes to migrate to warmer climes. Rowan (1931) has shown that the very low winter temperatures in Alberta are not by themselves fatal to small birds kept in outdoor aviaries provided that they are well supplied with food, and he has observed that food consumption goes up enormously in these conditions. Normally, of course, these birds would migrate southwards.

An important method of conserving bodily heat is the physiological one of storing up fat under the skin, and this has the additional advantage that the fat can be drawn upon in times of food shortage in winter, or during hibernation.

There is also the morphoplastic response of growing a thicker coat, a method seen especially in fur-bearing mammals, whose pelts are at their best in winter time. Even animals that do not normally grow a thick coat may do so when exposed to continued cold. It is stated by Hagenbeck (1909, p. 206) that giraffes allowed to winter out of doors in the Hamburg Zoo grow a thick crop of hair, which by the end of the winter is two and a half times as long as the normal coat.

We have, then, as means for preventing body temperature from dropping to dangerous levels, (1) the immediate physiological responses described above, (2) behavioural responses of many kinds, including an increased food intake, and (3) slow physiological and morphoplastic responses which help towards the conservation of heat. The goal—considered objectively—is the same; the means differ, but they are equivalent functionally, and complementary to one another. If the animal is unable to use one means of protection against a fall in body temperature, it employs alternative means. An interesting example of this is given by Cannon (1932, pp. 262-4). When the sympathetic system is put out of action in the cat, by the removal of the main ganglionic chains, the physiological responses to cold, consisting in the erection of hair, the contraction of the superficial blood vessels, and the increased secretion of adrenin, can no longer come into operation. 'The behaviour of such an animal in cold weather is consistent with this defective state. It exhibits a marked antipathy to cold air and to draughts. In the cold weather of winter

it crouches in the neighbourhood of sources of heat and leaves such places only at feeding time.' Besides keeping in the warm, the sympathectomized cat has only one other resource for keeping up its temperature, the action of shivering, and in cold surroundings it shivers far more than a normal cat. One cat during the year that elapsed after the removal of its sympathetic system came to rely more and more on shivering to maintain its temperature in a cold room, and managed by this means to keep it up to normal level.

Richter, in 1927, apropos of nest-building by rats, called attention to the functional equivalence of the different means of protection against cold in the following significant words: 'We may regard nest-building as a part of the heat-regulating mechanism, just as we consider the growth of fat and hair during cold weather a part of the more primitive physiological manifestations of heat conservation. Nest-building, like the building of shelters and the wearing of clothing, is a much more highly developed method of maintaining a normal body temperature, but it is nevertheless an expression of the same impetus that produces the increase in fat and hair in more primitive animals' (pp. 339-40).

Among poikilotherms protection against excessive cold may be achieved by behavioural action, as by burying deeply in the ground to a depth below the influence of frost, but many pass the winter in a state of cold rigor. In the hive of the honey-bee, however, cold rigor is avoided in winter by the generation and conservation of heat. When the production of brood is finished and winter approaches, the bees assemble between the combs in a dense cluster. By the movement of the bees within the cluster the temperature is kept up, in the centre, to a level of about 20-30° C., the energy required for this movement being

supplied by the winter stores of honey, or the sugar supplied by the beekeeper. This temperature is kept up even in extremely cold weather; Himmer (1932), whose account we follow, states that the difference between the air temperature and that of the centre of the cluster may be as much as 59°C .

When the external temperature is less than $7-8^{\circ}\text{C}$. the temperature of the centre is actively varied inversely with the external temperature in such a way and to such a degree that the temperature of the bees on the outside of the cluster is kept up to a level of $8-9^{\circ}\text{C}$. This temperature is sufficient to prevent them suffering from cold rigor (which sets in at $6-7^{\circ}\text{C}$.) and falling off the cluster. In cold weather the cluster is tight; in warmer weather the cluster is looser. In cold weather the bees use more of their food stores than when the weather is milder. When the air temperature rises above $7-8^{\circ}\text{C}$. heat regulation becomes unnecessary and the hive becomes poikilothermic. The first flights take place in the spring when the temperature has risen to 8°C . or more. This is, I think, the only case known where a poikilothermic species actively keeps up its temperature in the winter by appropriate behaviour, aided of course by the protection afforded by the hive. When the queen bee begins to lay, another cycle of heat regulation sets in, directed this time towards maintaining a steady incubation temperature for the brood.

The warm-blooded mammal responds to excess production of heat, or to overheating from the atmosphere, primarily by physiological means, but also by taking refuge in shaded, cool and airy spots. Overheating produces through the sympathetic system a dilatation of the arterioles in the skin, whereby more blood flows through them and more is exposed to cooling through radiation and conduction, if the external temperature is lower than that

of the skin. The sweat glands are also stimulated to activity and a cooling effect is produced by evaporation, which is especially great when the outside air is hot and dry. Much heat is also lost through quickened respiration, whereby large volumes of warm moist air are expelled. The dog, which is deficient in sweat glands, cools itself down chiefly by this means, rapid panting causing a loss of heat through evaporation from the lungs and from the extended tongue.

'Many marsupials lick wide areas of the body...this extensive licking of the marsupials is merely a substitute for respiration... Many marsupials, such as opossums and kangaroos, when distressed by the heat, lick the whole of the fore limbs, and with increasing need for heat radiation moisten large areas of the body by means of licking with the tongue' (Wood-Jones, 1939, p. 230). This is a means of providing a surface of evaporation in the absence of sweat glands.

If these physiological 'mechanisms' are defective, then the animal exposed to high temperatures may die of heat stroke. Cannon (1932, p. 264) relates how a monkey deprived of its sympathetic chains and placed outside on a warm day in June showed a great rise in temperature and eventually succumbed to heat-stroke.

The warm-blooded mammal cannot long survive a body temperature several degrees above its normal. Collapse occurs in man at about 42°C . and in the rabbit about 43°C ., some 5°C . above the normal body temperature.

Heat stroke and death may occur also in poikilotherms, as the following observations on reptiles show.

That snakes and lizards become torpid in cold weather is well known; that they are adversely affected by high temperatures is shown by the investigations carried out by Cowles and Bogert in the Colorado Desert in California (Bogert, 1939). They found that small lizards succumbed

very rapidly when exposed to a hot sun on sand having a temperature of 57°C . Larger lizards of desert-living species withstood such temperatures for 15 or 20 minutes, but when their body temperature reached 47°C . they also perished. Most of the desert snakes hunt by night, but the slender fast-moving Red Racer is often seen abroad in the daytime. Cowles and Bogert exposed it in an area without cover having a ground temperature of 50°C ., and found that it was not able to traverse more than 80–90 yards before being overcome by the heat. Some $6\frac{1}{2}$ minutes after exposure it was motionless and apparently dead, with a body temperature of 46°C . A small rattlesnake, the Sidewinder, died in 12 minutes with a body temperature of 45°C . when exposed to hot sun on hot ground. Bogert regards 49°C . as the absolute maximum which any reptile can endure, even for a short period.

How then do snakes and lizards in hot countries, and especially in deserts, contrive to avoid heat-stroke? They have no physiological method of regulating their body temperature, except that some lizards are able to change colour from dark to light on exposure to the heat of the sun, thus reflecting some of the heat. Both snakes and lizards in the Colorado Desert avoid excessive heating through appropriate behaviour. Some hide by day in cool places or burrows, and come out for food only in the dusk and the night. Lizards that feed by day bask in the hot sun only for short periods, retiring to the shade to cool off; others live and feed in the shade of the canyons. The poisonous Gila Monster (*Heloderma*) batters on birds' eggs during the spring, storing up fat in its tail, and spending the summer in a dormant condition in the cool depth of a burrow.

The Sidewinder snake hunts extensively at night, but by day is to be found under cover, often in the burrows of

kangaroo rats. Cowles and Bogert kept a number of these snakes in an enclosure provided with a number of pipe burrows sloping into the ground. They observed that as the day grew hotter the snakes retired farther down the pipes. Taking records of the snakes' temperature they discovered the remarkable fact that it remained constant throughout the day. 'The first temperatures taken in the morning were exactly 92° (34.4° C.) for every specimen in the cage. An hour later they were the same. By the hot part of the afternoon every Sidewinder had moved deeper in the pipe as the air grew warmer, and had to be drawn out with a hook. Again when temperatures were taken each Sidewinder was found to have maintained his body temperature at exactly 92° . On subsequent days a variation of no more than one degree was ever recorded' (Bogert, p. 34). This snake accordingly keeps its temperature close round what is presumably a comfortable optimum by shifting its position towards the cool as the air grows warmer. Probably other reptiles also have a 'preferred' temperature at which they try to remain; in this way they make an attempt at thermoregulation (see Cowles, 1940; and Gunn, 1942, p. 307).

Not only snakes and lizards but small mammals also avoid the excessive heat of desert conditions by appropriate behaviour. Many are nocturnal, and spend the day in deep burrows in a zone where the temperature is moderate and constant and humidity sufficient. Most of the small rodents fall into this category—the jerboas, gerbils and spiny mice. 'Many of the small wild rodents close the mouths of their burrows by day with a plug of earth, and no doubt this tends still further to stabilize the climatic conditions which prevail in the burrow' (Buxton, 1923, p. 103).

In many social Hymenoptera the temperature of the

nest is partially regulated, and excess of heat avoided, by behavioural action (Wigglesworth, 1939). 'Among ants this consists only in opening and closing the entrance to the nest according to the temperature, and in selecting the site for the nest—under stones or with a cap of earth to collect and retain the heat of the sun. The wasp *Polistes* likewise obtains the heat necessary for its brood by solar radiation as well as from the air; but if the temperature becomes excessive, it cools the nest by fanning with its wings (at $31.5\text{--}35^{\circ}\text{C.}$), and often combines this with bringing water and applying it to the comb (at $34\text{--}37^{\circ}\text{C.}$). *Vespa* also brings water to cool the nest by evaporation, or it may use fluid which it causes the larvae to emit. In *Apis*, the hive is maintained during the summer at a temperature around $34\text{--}35^{\circ}\text{C.}$ If it rises above this it is cooled by fanning and perhaps by the carriage of water' (p. 360).

7. PROVISIONAL CONCLUSIONS REGARDING RESTORATION OF NORMS .

The few but diverse examples of the restoration of structural and functional norms which we have considered are by themselves sufficient to suggest the existence of an empirical law, which may be provisionally formulated as follows: *If in a living animal normal structural and functional relations, either external or internal, are disturbed, activities will usually be set in train that are directive towards restoring structural and functional norms, or establishing new norms which are adapted to the altered circumstances.* The law cannot be stated in absolute terms; we might find that in certain cases restoration of the normal did not take place, or that the disturbance was far too great for compensatory activity to be effective—as for instance in cases of mortal injury. The law is purely empirical and its extent and validity can only be found out by experience. I suggest, however, that it has

wide though not universal validity, and that it is of value as a generalisation of observed and observable fact. It does not imply that the activities concerned are purposive or purposeful in the sense of being intelligently directed to ends; it merely states the fact that these activities usually tend towards restoring normal relations.

We have seen that the activities concerned in the maintenance, restoration and adaptation of norms are of three main kinds, which we may distinguish as behavioural, physiological and morphoplastic. Behaviour implies directive movements, whether of the animal as a whole or of its cells; in higher animals it depends upon an elaborate organisation of receptors, transmitters and effectors, upon an intricately co-ordinated neuro-muscular system. In such animals physiological activity too is mediated by an elaborate organisation of organs under neural and hormonal control, and it might well be described as a kind of internal behaviour. But physiological activity comprises also simple organ and cell activities, such as restoration and excretion. I call 'morphoplastic' such activities as result in a more or less permanent change in form, usually by way of growth, multiplication and differentiation.

As examples of these various kinds of activities we may take (1) the behaviour of *Molanna* in repairing its case, and the active migration of cells in the wound-healing of *Rhodnius*, (2) the physiological regulation of body temperature in mammals, and the secretion of cuticle in *Rhodnius*, the first two being behavioural, the second two physiological; as examples of morphoplastic change we may adduce (3) the growth of hair as a response to cold, and the multiplication of cells in the healing of wounds; degeneration of unwanted cells may also be regarded as a special kind of morphoplastic response.

These various modes of response are *functionally* equi-

valent; they are different means or methods of attaining the same end. This we saw very clearly in our discussion of the various ways in which a warm-blooded animal keeps up its body temperature (pp. 35-39). We saw too that when one method of response to cold was put out of action, alternative methods were used to compensate for the deficiency. In the process of wound healing, migration and proliferation of cells are complementary and equivalent methods of closing up the exposed surface and restoring the normal density of cells (p. 17). If the amount of liver tissue is diminished by experimental means, it is restored, according to circumstances, either by regeneration or by hypertrophy, which are functionally equivalent processes. *Molanna* repairs injury to its case by its own behaviour; in *Rhodnius* epidermal injuries are repaired by the activities of its cells.

Reverting to our tentative formulation of the law of the restoration of norms, let us see whether we can analyse the relations to which it refers. In this endeavour we can obtain great assistance from an unexpected source, namely, from the masterly study of psychological principles with which H. A. Murray (1938) introduces a co-operative investigation of human personality undertaken by the Harvard Psychological Clinic.

For a simple behavioural act with a clear-cut beginning and end Murray suggests the following convenient formula:

$$BS \rightarrow A \rightarrow ES,$$

'where *BS* stands for the conditions that exist at the initiation of activity; *ES* for the conditions that exist at the cessation of activity; and *A* for the action patterns, motor or verbal, of the organism' (p. 55). Generalising this formula, we may use it to describe what happens in all activity directive towards the restoration of norms, *BS*

standing for the conditions at the beginning of behavioural, physiological or morphoplastic activity, *A* for the activity itself, and *ES* for the end-state which marks the cessation of activity.

We have already seen the importance of the *ES* or end-state, to which the activities of restoration are directive; the *BS* in the examples we have studied is, expressed in general terms, a disturbance of, or deviation from, a normal functional or structural state. Here we must introduce another concept, that of stimulus situation (*SS*), which we shall take over in modified form from Murray. He defines *SS* as 'that part of the total environment to which the creature attends and reacts' (p. 749). He is dealing, of course, with psychological activity, and the definition is couched in psychological terms, which are not obviously applicable to organic activities in general. But we can broaden the definition so that it reads 'that part of the environment of the organic agent to which it reacts'. This extends the concept to cover the responses—of any kind, not merely behavioural—made by internal agents, such as cells, as well as behavioural responses by the animal as a whole. It leaves undecided the question whether or not the stimulus-element in the environment, either of cell or of organism, is sensed or perceived. In the behaviour of the whole animal we have every reason to think that it does sense or perceive and attend to significant objects and events in its environment, both external and internal, but we can assert nothing with certainty, one way or the other, about the possible sensations of its cells.

Defined in this broad and general way, the *SS* comes in as a link between the *BS* and *A*. For example, it is not the mere occurrence of a wound (*BS*) that directly initiates the activation and migration of cells in wound healing, but a particular *SS*, namely, the appearance of the products of

protein disintegration, as a result, normally, of the injury to cells caused by wounding. It is this that stimulates the neighbouring cells to directive migration. We have already noted that this stimulus is 'normally adequate' (p. 16). We must note too that this specific response to the disintegration products of proteins implies that the cells which react are, we might say, 'predisposed' or pre-adapted to respond to this particular stimulus in this particular manner. They have a specific *action-disposition*, coupled with a specific *stimulus-disposition*. They themselves are to be regarded as *agents*, showing receptive and executive activity. The value of the *SS* concept is very clear in animal behaviour, and we shall have frequent occasion to return to it. But in many of the examples which we have considered it is not possible to point to a positive external *SS* to which response is made; often it appears that the agent is moved to activity by the *lack* of something which is normally present in its environment, external or internal. *Molanna* is stimulated to repair its case when some part of it is missing; the epidermal cells at the edge of a wound are stimulated to spread out over the wound when they are without contact at the free edge; *Microstoma* actively ingests, and its cells transport to the surface of its body, additional nematocysts when the full complement of these are not present; a beetle or a starfish is moved to re-establish effective contact when a firm support is missing.

We have seen some very remarkable examples of how the animal supplies what is lacking or needed to restore normal functional and structural relationships, especially noteworthy being the action of *Microstoma* and its cells in providing the normal number of nematocysts, rejecting these when it has enough, and ingesting the flesh of *Hydra* when food need is dominant. Even more remarkable are the cases we have noted where what is superfluous, or

unwanted, for normality is destroyed—surplus cells in the new-grown epidermis of *Rhodnius*, excess of erythrocytes in the hypertrophied erythron, superfluous pieces of the tube in *Molanna*.

There is, one begins to see, a close relation between norms and needs. In our formulation of the law of the restoration of norms we have allowed for the fact that norms may change in adaptation to altered circumstances. This may often mean 'in response to altered needs'. A beautiful illustration of this is provided by the behaviour of the erythron, which is increased or diminished in size in strict accordance with the varying needs of the animal for oxygen (pp. 27–30). Also the amount of liver substance is regulated according to the demands made upon it.

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DIRECTIVE ACTIVITY IN THE SATISFACTION OF METABOLIC NEEDS

As a first example let us consider the ways in which the living animal ensures to itself a supply of oxygen adequate to its needs.

1. OXYGEN NEEDS

First a few examples of response to lack of oxygen by simply organised animals. According to Jennings (1906, p. 66), *Paramecium* does not generally collect round a bubble of air or oxygen introduced under the cover-slip, but if the preparation is sealed so that air is excluded, and is kept for some time, the oxygen becomes much reduced except near the bubble, and the *Paramecia* now collect round it. They do this by carrying out avoiding reactions to the zone of reduced oxygen. The *BS* is presumably a state of lack of sufficient oxygen for functional requirements, the *A* is a simple form of behaviour, and the *ES* a restoration of normal supplies. What the *SS* is remains obscure. This kind of behaviour is common in Infusoria.

In *Arcella*, the little shelled rhizopod, the response to lack of oxygen is physiological, rather than behavioural. When the dissolved oxygen in the water in which it lives is reduced below a certain point, its invariable response is to secrete gas bubbles of oxygen, in its substance, which reduce its specific gravity and float it up to the surface, where oxygen is normally plentiful (Bles, 1929). The water at the bottom of a pool, where *Arcella* normally lives, is

liable to be poor or lacking in oxygen. 'Hence it will clearly benefit those aerobic or semi-anaerobic organisms which live on the bottom to have a means of escape which will rapidly carry them from a level of oxygen depletion to a level of oxygen plenty. The principal stimulus to form gas-vacuoles in *Arcella* and similar organisms which live at the bottom of ponds and ditches is lack of oxygen' (p. 561). The response is directive towards remedying the lack of oxygen.

Behavioural response to oxygen concentration is shown by the various species of *Hydra*—and of course by many other aquatic animals. *Hydra* is found usually near the surface, and it has been shown that this is not a gravity response, but a response to oxygen (see Jennings, 1906, p. 216). Beutler (1933) reports an interesting difference between the brown *Hydra* and the green in this respect; the former is always sensitive to oxygen concentration and seeks out the areas richest in oxygen; the latter, being provided with oxygen in the light by the photosynthetic activity of its enclosed algal cells, shows this sensitivity only in the dark; the response is relative to need.

After these examples of simple responses to oxygen need, we may go on to consider some aspects of the very complex physiological and other activities concerned in ensuring an adequate supply of oxygen to the highly organised mammalian body.

I shall not attempt to give a full exposition of the physiology of respiration in man and the higher animals; this extremely intricate subject, on which so much work has been done in recent years, is treated in great detail in the comprehensive book by Haldane and Priestley (1935), from a functional or biological point of view which is very similar to that advocated here; it is dealt with, also in terms of norms and needs, in a very illuminating way by

Cannon (1932, chap. x), especially in its relation to the maintenance of homeostasis, or a steady state, in physiological activity in general; it is therefore unnecessary, and it would be presumptuous for a non-expert to try, to deal with the subject in any detail. I shall limit myself to a simple account of the various ways in which the mammalian organism satisfies its varying needs or functional requirements for oxygen, and accommodates itself to a lessened supply, referring the reader for details to the works mentioned.

The need for oxygen is continuous, though the amount required varies greatly according to functional demands, and oxygen is normally in plentiful supply. There is no provision for storage, beyond the limited amount always present in the lungs, and a complete cessation of supply is very quickly fatal. In these respects, the need for oxygen differs very markedly from the need for food, which is periodic and can be satisfied for a time by sufficient intake; excess supplies can also be stored and drawn upon as required, and complete absence of food does not entail immediate death.

Oxygen is, of course, a fundamental requirement for cellular activity, and it is the needs of the tissues that ultimately determine its uptake. It is, however, important to remember that respiration is a twofold process; there is a taking up of oxygen, but also a giving off of carbon dioxide in similar amount. We shall see that the production of carbon dioxide in excess of a norm is one of the most important factors concerned in the regulation of breathing and the supply of oxygen to the lungs and the tissues. Even when the animal is at rest, carbon dioxide is constantly being given off by the tissues and being accumulated in the blood, to be released to the air in the alveoli of the lungs. Its percentage in the alveolar air therefore tends

to increase. Now it has been found that as soon as this percentage increases, even slightly, above a certain normal, the respiratory centre in the medulla is stimulated to increase the respiratory movements, with the result that the slight excess of carbon dioxide is washed out, and the normal percentage restored; when this happens the rhythm of breathing returns to normal. Another result of the increased ventilation in the lungs is of course that more oxygen is brought in. Normal breathing, and the supply of an adequate amount of oxygen to the tissues in the resting animal, is mainly regulated in this way, though a reflex whereby inspiration leads to expiration, and expiration to inspiration, also comes into the story. The response of the respiratory centre is a very delicate one; it has been found that in man an increase of its alveolar percentage of carbon dioxide from 5·6 to 5·8 is sufficient to double the ventilation of the lungs, and conversely, a decrease to 5·4 brings about a temporary cessation of breathing, a state of apnoea.

These statements hold good if the barometric pressure is normal. If this is varied considerably in experimental conditions, the percentage of carbon dioxide in the alveolar air also varies, and it is its partial pressure that is regulated to constancy. Increase in the partial pressure of carbon dioxide in the alveolar air leads to an increase of it in the arterial blood, and a minute change in the hydrogen-ion concentration of the blood; it is this slight change, brought about by carbon dioxide, that affects the respiratory centre in the medulla and stimulates increased ventilation in the lungs, with as a consequence a removal of excess carbon dioxide from the alveolar air and an increased supply of oxygen to the alveoli. The response of the respiratory centre to an excess of carbon dioxide in the arterial blood has then the effect of increasing the

supply of oxygen to the lungs, though it is not a direct response to lack of oxygen. It should be noted that the regulation of the hydrogen-ion concentration of the blood is almost as important for the maintenance of life as the supply of oxygen to the tissues.

In muscular activity, the oxygen requirements of the body are greatly increased, and much more carbon dioxide is produced. How does the body cope with these two problems—the need for more oxygen, and the need for getting rid of the excess carbon dioxide? In answering this question, we cannot do better than follow the admirable account given by Cannon (1932) of the regulatory activities which are set in motion.

When a man engages in violent exertion his oxygen requirements rise far above what can be immediately supplied by his lungs; he incurs therefore an 'oxygen debt', which can only be paid by continued deep respiration for some time after the muscular activity has ceased. This serves to oxidise to carbon dioxide or to reconvert into glycogen the lactic acid which has been produced as a result of muscular contraction and has accumulated during exertion. In moderate activity the increased oxygen requirements can be met as they arise and oxidation of waste substances can keep pace with their production. 'To supply the need for extra oxygen during muscular work', writes Cannon, 'the functioning of the lungs, the heart and the blood vessels is modified in various and complex ways, each directed towards providing an amount of oxygen sufficient to meet the requirements of the labouring parts or to pay the oxygen debt if the requirements have not been met during the period of labour' (p. 148).

These directive modifications of normal activity are many and subtle, and we can consider them only in outline. Breathing becomes deeper and more frequent, so that the

pulmonary ventilation is greatly increased, perhaps up to 10 times its normal amount. This change is at first cortical in origin, but is mainly caused by the response of the respiratory centre to the increased pressure of carbon dioxide in the arterial blood, which is a result of muscular activity. As we have already seen, this increased ventilation brings in more oxygen to the lungs and washes out the excess carbon dioxide. 'By the operation of this admirable automatism the percentage of oxygen in the alveolar air, and hence its diffusion pressure into the blood, is maintained at or slightly above the normal level, although there may be a five- or tenfold increase in the use of oxygen in the vigorously active body' (p. 153).

Through the action of the sympathetico-adrenal system, the ring muscles in the bronchioles relax, thus facilitating the passage of air in and out of the lungs.

There are also adaptive changes in the circulation. Both the rate of beat and the stroke volume of the heart increase considerably, and may be doubled, thus supplying to the tissues a greater number of oxygen carriers (erythrocytes) per unit of time, and increasing the number of trips they make between the lungs and the active tissues. The increased rate of circulation is greatly helped by the contraction of the blood vessels of the stomach and intestines, by the pumping out of blood from the active muscles during their contraction, and by the pumping action of the diaphragm, which facilitates the return of blood to the heart from the great veins. 'Note the nice economy of this organisation in the body. The contracting muscles which need extra oxygen because of their contractions, automatically favour the securing of the needed oxygen by returning the blood which carries it. And the diaphragm, which, as we have seen, is made to pump more vigorously during exercise, not only maintains in the lungs the oxygen

supply for loading the oxygen carriers, but also aids to speed up the circulation of the carriers and thereby to augment their delivery of oxygen to 'the needy tissues' (p. 155).

The increased heart beat is due partly to the suppression of the vagal check and partly to the stimulation of the sympathetic nerves supplying the heart. There is evidence that the nerve centres concerned may be stimulated in the same way as the respiratory centre, by an increase in the carbon dioxide pressure, and Cannon concludes therefore that 'In vigorous muscular work, the remarkably close correlation between the adjustments of the respiratory and the circulatory systems to the needs of the organism may thus be explained; though both systems are started into faster action by impulses incidental to a voluntary movement, they are maintained in the performance of their extra task by the increased concentration of carbon dioxide in the arterial blood. Later they gradually return to their quiet routine functions, because their extra activity has resulted in reducing the carbon dioxide to the resting level' (p. 159).

Assisting the supply of blood and oxygen to the tissues during activity there is a dilation of the arterioles and capillaries. It has been shown by Krogh that in a resting muscle only a small number of the capillary vessels are open and functioning at any one time, whereas in an active muscle they are all in action, thus enabling advantage to be taken of the heightened arterial pressure which results from the increased action of the heart. It is not known for certain what is the stimulus for the opening of the capillaries; it may be local lack of oxygen, or increase of carbon dioxide, or the presence of some substance resulting from the wear and tear of the active muscle.

Increased speed of circulation through the capillaries

means that there is less time for each oxygen carrier to unload its oxygen, but this disadvantage is more than compensated for by the physico-chemical fact that increase of carbon dioxide and rise in temperature both accelerate the discharge of oxygen from oxyhaemoglobin, and both these conditions are found in active muscle. The effect of the increase in the number of trips between lungs and tissues made by the oxygen carriers, which is due to the increased rate of circulation, is enhanced by the more rapid and fuller utilisation of the oxygen they carry.

Provision is also made for an increase in the number of red corpuscles in circulation during muscular activity. It has been shown by Barcroft that the spleen acts as a store for blood corpuscles, and that, when an extra supply is required by the body—as for example after severe haemorrhage (see p. 29)—they are squeezed out into the circulation by contraction of the muscles of the spleen. In the cat, exercise may result in the discharge of as much as 13 g. of fluid rich in red corpuscles, which go to augment the supply of oxygen carriers, at a time when they are needed.

These are, then, in the most general outline, the main ways in which the body responds to the need for more oxygen which is set up by muscular activity, and gets rid of the excess carbon dioxide which is produced. Interoceptive and interoceptive 'mechanisms' are chiefly concerned—what I have called (p. 45) the 'internal behaviour' of the organism. It is of special interest to note that the most important stimulus which leads to these regulative activities is a byproduct of cellular activity, carbon dioxide. This might be regarded as a 'sign-stimulus' for action, just as the products of protein-disintegration consequent on injury serve as a sign-stimulus for the activities of wound-healing. It acts by altering the normal pH of the blood.

Let us consider now what happens when, for any reason, the supply of oxygen required for normal functioning is deficient. In our discussion of the regulation of the erythron (pp. 27-30) we have already mentioned the main causes which lead to such deficiency of supply, namely, extensive haemorrhage, poisoning by carbon dioxide, defects in the respiratory and circulatory systems, reduction of the diffusion pressure of oxygen in the inspired air, and we have noted the very remarkable fact that in such circumstances one main method of compensation is an increase in the number of erythrocytes, by new production from the bone-marrow. We have seen that the number of functional erythrocytes in circulation is nicely adjusted to the needs of the tissues for oxygen, additional ones being provided as required, and any excess over what is needed being destroyed. Increase in the number of erythrocytes is the chief means by which the body adapts itself to life at high altitudes, where oxygen pressure is reduced and its supply to the tissues is therefore difficult. Other, more immediate, responses to a deficiency of oxygen in the air are, for example, an increase in respiratory and circulatory action, or a movement into purer air, as when a man leaves a stuffy room or opens a window. It appears also that when an animal is made to live in air containing only 10 % of oxygen hypertrophy of the lung may be induced (Boycott, 1932, p. 7).

Looking at the whole matter very broadly, we may say that the methods of response to a temporary or permanent deficiency of oxygen, *relative to the functional needs of the moment*, are threefold. There is the simple method of moving away from a region deficient in oxygen to one where oxygen is more plentiful, as exemplified by *Paramoecium*, *Arcella*, and man, and of course by a vast number of other animals. There is the method, exemplified most

admirably in the higher mammals, of immediate physiological responses of an elaborate character, an internal behaviour directive towards increasing the supply of oxygen to the tissues, including the discharge of reserve erythrocytes from the spleen. Thirdly, there is the much slower response, of a morphoplastic character, consisting in the increased production of new erythrocytes in the bone-marrow and their release into the circulation, where they are required as additional oxygen carriers; the lungs also may hypertrophy.

The general rule or law regarding oxygen needs and their satisfaction may be formulated as follows. *If the supply falls below what is necessary for immediate functional requirements, behavioural, physiological or morphoplastic activities, or a combination of them, will be set in action that are directive towards remedying the deficiency.* The modes of response to oxygen deficiency vary with the degree and type of organisation of the animal; they may be simple or elaborate; they do not usually imply consciously purposive action, though in man and probably in many other animals the behavioural effort to remedy oxygen defect is excited by a feeling of discomfort or suffocation. In such cases, a feeling may be the real SS that leads to action.

2. THE NEED FOR WATER

In man a feeling of thirst is the effective SS that leads to the drinking of water or other fluids, though of course other psychological factors may lead to drinking when a real need for fluid is absent. The sensation of thirst is, according to Cannon (1932), chiefly localised in the mouth and throat, and is due to a decreased secretion by the salivary glands, resulting from a shortage of water in the body, and inducing a feeling of dryness and stickiness. The immediate symptoms of thirst can be temporarily relieved

without meeting the body's need for water, if the flow of saliva is stimulated. But normally the need for water is indicated or signalled by a sensation of thirst. Thirst is acute when through loss of water in violent exercise or through excessive haemorrhage the normal quantity of water in the body is considerably reduced, and the main response is the behavioural one of drinking water. But this is only part of the story.

The amount of water in the mammalian body is regulated in accordance (1) with metabolic needs, and (2) with the need for keeping the water content of the blood constant, and it depends upon a balance between the intake of water by the mouth and the output through the kidneys, the skin and the lungs. Physiological responses as well as behavioural are intimately concerned in this regulation of water balance.

(1) It has been shown by Richter (1938) that the voluntary intake of water by man and various other mammals is a function of body surface rather than body weight, and is hence related to metabolic rate. In agreement with this relation is the fact that in rats receiving thyroid extract the increased metabolism so produced is associated with an increased intake of water. Conversely, removal of the anterior lobe of the hypophysis, which reduces the metabolic rate, leads to a marked decrease not only in food intake but in water intake also (Richter, 1936*b*, p. 399).

The regulation of the water balance necessary for metabolism is largely effected by the secretion (pituitrin) from the posterior lobe of the hypophysis (refs. in Richter, 1938). Pituitrin has a marked anti-diuretic effect, and it has been found that loss of water, producing dehydration, induces a greater secretion of pituitrin, and hence a diminution of the output of water through the kidneys. On the other

hand, if the water intake is increased beyond normal, the secretion of pituitrin is decreased, and more water is excreted. Drinking of water also helps to maintain or restore the water balance, though it seems that the secretion of pituitrin plays the more important part. There are therefore two functionally equivalent methods of regulating water balance—one physiological, the other behavioural. Now Richter has shown that if the pituitrin effect is put out of action, by removal of the posterior lobe, the result is a greatly increased diuresis and loss of water (resulting in a state of diabetes insipidus), which is, however, accompanied by an increased thirst and an increased drinking of water. 'In animals with total removal of the posterior lobe... the maintenance of the water balance is dependent entirely on the voluntary ingestion of water' (1938, p. 674). Accordingly, when the physiological method of regulation is rendered impossible, the behavioural comes more fully into play and compensates for the physiological defect.

(2) The water content of the blood is held remarkably constant, and it is little affected either by the drinking of large quantities of water or by complete deprivation of water. Dogs kept for 3 days without water showed no diminution in the percentage of water in the blood, and conversely the drinking of nearly 6 quarts of water in 6 hours by human subjects led to only a barely appreciable dilution of the blood. The main regulation is effected through the action of the kidneys, which quickly get rid of excess water in the blood, and slow down their action when water has to be conserved. There is also another way of preventing the dehydration of the blood, and that is by utilising the water stored in the muscles and connective tissue spaces. 'If water is drunk in a large amount, it is not allowed to dilute the blood, but is either reserved in the connective tissue spaces or discharged via the kidneys.

And the losses of water from the body by sweating, by breathing, by the secretion of urine, or by temporary escape into the alimentary canal, likewise do not alter the composition of the blood to a noteworthy degree. Under these circumstances it is kept uniform by contributions from reserves in the tissues' (Cannon, 1932, p. 89). This leads of course to a dehydration of the tissues, and a diminution of the secretion from the salivary glands, which, as we have seen, causes a sensation of thirst and the consequent drinking of water, if such be available. This in its turn leads to the replenishment of the depleted stores of water in the body, and the restoration of a normal state. Here again we see physiological and behavioural activities co-operating as functionally equivalent methods of reaching the same biological goal, in this case the maintenance of the normal water content of the blood and of the body as a whole. In the behavioural mode a sensation (thirst) appears to be an essential element in the response.

3. FOOD NEEDS

The natural food requirements of an animal are as a rule somewhat specialised. Many are carnivorous or insectivorous and feed only on living prey; others feed by choice on dead and decaying flesh, others on blood. Many are herbivorous, and specialise on grass, or grains, or leaves, or roots and so on. Specialisation may go so far that the animal will eat only one kind of plant or one kind of animal, or a very restricted number of kinds. The caterpillar of the Cinnabar moth (*Tyria jacobaeae*), for instance, is limited in natural conditions to the ragwort (*Senecio jacobaeae*) and the groundsel (*S. vulgaris*) as food plants (Cameron, 1935). The little marsupial 'bear' or koala (*Phascolarctus cinereus*) will eat nothing but eucalyptus leaves and bark, and out of the hundreds of species of eucalyptus

found in Australia each local race of koala restricts itself to four or five, with an occasional change to one or two more (Pratt, 1937).

Our first question must be—how does the animal find the particular food or foods appropriate to it, those that satisfy its special needs? The general answer is that it has a hereditary or innate predisposition to attend to and perceive particular sensory signs which are normally adequate as indicative of the proper food. Let me illustrate this rather summary statement.

In the simplest case, the animal is guided by the specific smell of the food. This is so with the koala, which in the wild state 'selects its food by sniffing the leaves of individual trees which it climbs, one after another, until the right tree and the right leaves are found' (Pratt, p. 116).

The dung beetle (*Geotrupes*) finds its food entirely by smell (Warnke, 1931), scenting it by means of its antennae at a distance of 4 metres if the wind is right, and searching in the direction of the smell till it finds the dung. Ammonia, skatol and indol, in that order, exercise a similar attraction to dung, of which they are, of course, constituents. The sacred beetle *Scarabaeus*, which makes balls or pellets of dung and rolls them away to be buried for future consumption, recognises the substance solely by smell, and can easily be tricked into treating as a pellet of dung any small object such as a chestnut, or a ball of dried *Posidonia*, or even a little ball of lead wrapped up in cloth, provided it is smeared with dung (Heymons and v. Lengerken, 1929). The primary valent characteristic of the natural food and the pellet is its smell.

The whelk (*Buccinum undatum*), which feeds on dead and decaying animal matter, finds its food mainly by smell, the receptor organ being the osphradium, which is situated in the mantle cavity near the origin of the siphon (Brock,

1936). A slow current of water passes through the siphon over the osphradium. In the still water of an aquarium the juices diffusing from a piece of food not too far away reach the osphradium and excite the whelk to movement; it creeps in a winding and irregular path in the direction of the food, swinging the siphon from side to side in a probing and testing movement, and reaches the food in a few minutes. In natural conditions, in moving water, the whelk moves actively up-current if the water passing over the osphradium carries indications of food, and is thus guided directly towards the food.

A similar 'positive rheotaxis', which is really a seeking for food, is shown by *Planaria alpina*, which when immature is indifferent to a slow current of water. If in such conditions it is 'momentarily stimulated by a dilute solution of food extract (*Gammarus*) it responds by becoming positively rheotactic, and for 40-60 min. will continue to respond by moving upstream.... The stimulus from the food extract can only last for a few seconds, but the animal is instantly aroused and appears excited and reacts positively to the current' (Beauchamp, 1937, p. 112). Many dilute chemical solutions will also elicit an upstream movement in weak currents, but the animals react more vigorously to food extract than to anything else of this kind (Beauchamp, 1935, p. 280). As in *Buccinum*, food is found through positive response to currents bearing chemical signs of food, which are perceived through smell, or, more generally, chemical sense.

It is unnecessary to multiply examples of food finding by smell; let us turn to other sensory signs of food.

By many animals of 'visual' type, objects seen to be in motion are treated as potential food, provided they are neither too small nor too large. This holds good especially for animals that feed on living and active prey, of carni-

vores and insectivores generally. Instances are legion, and I need adduce only a few. The shrikes (*Lanius*), which are carnivorous in habit, eating all manner of small living prey, show a strong propensity to pick up any small object that moves. Miller (1931), who has studied the American species minutely, writes of them as follows: 'Animals which are captured, it is believed, are located largely by the detection of their motion, either in the air or on the ground, but principally the latter. In captive birds any flying, crawling or moving thing draws attention and usually pursuit. Thus, a dead mouse is far less exciting to a shrike than a live mouse. Moths or flies in the cage are pursued vigorously. In adults, until it is learned that a particular kind of inanimate object is edible, such an object is not often picked up in the bill... Evidently, a shrike to some degree learns to recognize suitable food materials by "trial and error". However, *anything that moves rarely proves to be unsuitable food and an adult uses motion as the most reliable criterion of food*'* (pp. 210-11).

The 'fighting fish' (*Betta splendens*), which is a visual feeder, treats any small moving object as possible food, snapping even at sinking grains of sand or at drops of moisture slipping down the outside of the aquarium wall (Lissmann, 1932). Form and colour are unimportant; any moving object is liable to be seized, if it is not too big to be taken into the mouth; taste and possibly tactile sense determine whether it is swallowed or rejected.

Many dragon-fly larvae attempt to seize any small moving object within reach of their labium, whatever this object may be. When an *Agrion* larva is hungry it will respond actively to any small object in motion, whether this be a small oligochaete or a little plasticine or metal ball waved on the end of a wire (Sälzle, 1932). The larva

* Our italics.

of the water-beetle (*Dytiscus*) shows the same sort of behaviour towards moving objects (Blunck, 1924). It reacts to any actively moving object in its vicinity by attack or by flight, according to the size of the object. Normally it lurks for its prey, leaping upon any small moving object that comes within its field of vision; it pays little attention to slowly moving objects such as a water snail.

The wolf spiders, according to Homann (1931), respond to motion rather than to form. *Pisaura* turns towards all small moving objects, whether they be insect prey, or models of such, or even moving shadows. It will orientate towards small balls of black wax in motion, or to the moving end of a grass stem. To a motionless fly it is indifferent, but if the fly moves it is immediately noticed.

An interesting case where both visual and olfactory signs are utilised in the capture of prey is given by Tinbergen (1932, 1935). The solitary wasp (*Philanthus triangulum*) provisions its nest exclusively with honey-bees, which it catches on the wing. Flying over its hunting grounds, the wasp is attracted to any bee or similar insect moving through the air within some 30 cm. range; it orientates towards the insect and hovers near, taking its scent. If it is a humble-bee or a fly or a beetle, it has no bee-scent and is generally left alone, but if it is a honey-bee, it is seized and carried off. The 'formula' for prey is therefore a simple one—any flying thing of approximately the right size is possible prey; discrimination between the right prey and the wrong is made by smell.

We see from these few examples that motion is often a sufficiently adequate sign of food. Objects that move are usually, though not always, alive; if an animal treats as possible prey any moving object of suitable size, the chances are that, in normal circumstances, it will not often be deceived; motion is *normally* adequate as a sign of possible

food. Decision as to the nature of the moving object when captured is made through smell or taste. Size is, of course, important as well as motion—size relative to the predator. Moving objects, too large to be eaten, often have danger-valence, arousing defence or flight responses.

A warm moving object has food valence for certain boas—those provided with labial pits (Noble and Schmidt, 1937). Specimens of *Boa hortulana* discriminate between a hot and a cold electric bulb which is swung past them at a rate of about 40 times a minute, striking only at the warm bulb; the response is best shown when the snake is blindfolded. Warmth without movement evokes no strike from the blindfolded boa. Species of *Boa* without labial pits do not show this response to a warm moving object, and direct experimental evidence demonstrates that these pits are the thermoreceptors concerned. The 'pit vipers' or Crotalidae of America also show when blindfolded the same response to a warm moving object, perceiving temperature difference and air currents by means of their facial pits. Many crotalid snakes are crepuscular or nocturnal in habit, and their temperature sense aids them in striking at warm-blooded prey in dim light or darkness. Vision, and to some extent smell, are also concerned in food finding, but 'in the absence of vision the labial pits of Boidae and the facial pits of Crotalidae are the most important sensory mechanisms for directing the strike towards warm-blooded prey' (Noble and Schmidt, 1937, p. 287).

Heat alone may be a normally adequate sign of food in the case of many animals, such as the medicinal leech, bugs, mosquitoes and lice, which suck the blood of avian or mammalian hosts. Take for instance the blood-sucking bug (*Rhodnius prolixus*), whose behaviour in search of food has been studied by Wigglesworth and Gillett (1934). It is aroused to attention by the proximity of a heated tube,

erecting its antennae and cleaning them with its forelegs; it then wags them alternately, in semaphore fashion, and advances straight towards the tube. 'As soon as one or both antennae touch the tube, the proboscis is extended and pressed vigorously against its surface.' The response is to the warm air diffused from the heated tube. Smells plays a small part in the finding of the natural host, and it is possible that vision and perception of vibration are also concerned to some slight extent, but the temperature response is the important one.

Howlett (1910) has shown that the females of several kinds of mosquitoes are attracted by heated air currents, and not by the smell of blood or perspiration. They tend to hover in the column of warm air ascending from any hot object, such as a pot of hot tea or the human head. The males, which do not suck blood, do not show this reaction towards heated objects. Females respond actively to a tube of hot water presented to them while they are confined in a gauze bag, 'stabbing with their proboscides through the meshes of the net, and displaying the utmost eagerness in their fruitless efforts to puncture the glass'. Further examples of sensory signs that are normally adequate as indicating appropriate food could be given, but there is no need to elaborate the point. The instinctive predisposition to attend to such signs is, of course, just one aspect of the integral specialisation and preadaptedness to a particular mode of life that characterises every kind of animal (see Russell, 1941, 1943).

As a general rule, these signs of food are non-valent, exciting no positive response, if the animal is full fed; some degree of food need, presumably experienced as hunger, is usually necessary before an animal will seek or ingest food, though eating beyond needs is not unknown. We know from our own experience that even tasty and succulent

meats may become actually distasteful if we are satiated with food. Feeding then, and the positive valence of food signs, normally depend upon need, and the effective SS is probably the sensation of hunger. If the need is great, and normal food is lacking, an animal will often try to eat food which it would normally reject, or even substances that are quite innutritious. If food is lacking altogether, and starvation sets in, physiological processes come into play which supply the minimal energy requirements for self-maintenance, by utilising the stores of fat and other substances previously accumulated in the body, and, in the long run, proteins from the living tissues themselves. The energy requirements in starvation are met by the oxidation of fat, carbohydrate and protein, which replace one another in proportion to the energy they liberate on oxidation within the body, as was shown by Rubner in 1883. 'Thus 1 gramme of fat furnishes as much energy as $2\frac{1}{4}$ grammes of protein or carbohydrate, and 1 gramme of fat from the reserve in the body takes the place of $2\frac{1}{4}$ grammes of protein or carbohydrate when the supply of the latter in the food is cut off. . . ' (Haldane and Priestley, 1935, pp. 5-6). The constant need of the animal for energy is therefore satisfied in two functionally equivalent ways, normally by the intake and utilisation of food, and, when food is lacking, by the utilisation of reserves in accordance with their energy value. What is needed is supplied by one means or the other, so far as is possible.

It is worth noting, too, that the storage of food reserves is achieved by two methods which are functionally equivalent. Some animals collect stores of food against the winter shortage; this is common among rodents; the vole *Microtus arvalis*, for instance, collects in the autumn bulbs and roots, 'which they store in chambers a few inches below the ground. These stores begin to be drawn upon

later in winter, so that the voles can stay indoors during the worst weather, without starvation' (Elton, 1942, p. 24). In other animals, especially those that hibernate, provision for winter scarcity is made by the physiological method of accumulating fat in the tissues.

An animal's normal or natural food clearly supplies its physiological requirements for proteins, carbohydrates, fats, mineral constituents and vitamins, and recent research has given clear indications that natural foods are adequate because they satisfy *specific appetites* for the particular food constituents that are necessary for survival, growth and reproduction.

Several experimenters have shown that various animals, such as pigs, rats and chicks, if given a free choice of a range of foods, select their meals in such a way that they thrive and show good growth, sometimes doing even better on a self-selected diet than on man-controlled rations. This was the case in the experiments carried out with chicks by Pearl and Fairchild (1921), and in the more recent work by Dove (1935), who found also that individual chicks differed considerably in their ability to make advantageous selections. 'When the same foods are given to animals for free selection,' he writes, 'the *wisest* will choose very different ratios and combinations of foods—to suit the demands of his genotype and the interaction of foods—than have been selected for him by the nutritionist and, in so doing, is able when the correct assortment of food is before him to select a combination that makes him superior to the animals fed by the present scientific methods of rationing' (p. 519). This choice is in the main instinctive. 'Choice of food is not entirely the result of experience and habit. In fact, the nutritive instincts are principally innate, "purposive" or directive reactions expressed with varying degrees of accuracy from the first contact with

food and altered with the altered demands of the organism' (p. 541). These and other experiments were carried out in the main with natural foods and such mineral constituents as occur naturally, and the results fall in line with the general fact that an animal is predisposed instinctively to select natural foods appropriate to its needs. The remarkable work of Richter, Holt and Barelare (1938) shows, however, that rats can select a most efficient diet from a range of pure food constituents, the vast majority of which they and their ancestors have never encountered in an isolated state before. Richter was led to undertake the experiments described below by the observation that rats rendered by operation deficient in salt or in calcium developed specific appetites for these substances, and remedied their lack by drinking large quantities of water containing salt or calcium lactate. 'It was decided then that if the deficient rats could select these two minerals to such great advantage, it might be worth while to determine whether normal rats could make wise selections of other minerals as well as of protein, carbohydrate, fat, and vitamins' (p. 735). Preliminary experiments were initiated to find out what were the most suitable pure substances to offer to the rats, and the choice fell upon the following representative food constituents: olive oil (fat), casein (protein), sucrose (carbohydrate), sodium chloride, 3 %, calcium lactate 2.4 % (calcium), dibasic sodium phosphate 8 % (phosphorus), potassium chloride 1 % (potassium), yeast (vitamin B complex), cod-liver oil (vitamins A and D), wheat-germ oil (vitamin E), and water. Eight female rats, about 50 days old, previously fed on the standard McCollum diet, were used in the self-selection experiment. They grew quite as well as on the McCollum diet, mated and gave birth to normal litters which they brought up successfully. They therefore made an appro-

priate selection of the materials offered them, one conducive to normal growth and activity and to normal reproduction. The average daily intake of solids was considerably less than in rats fed on the McCollum diet, partly because they ate far more fat and less protein and carbohydrate than are supplied in the McCollum rations. Their consumption of mineral constituents and of vitamins was of the same order as in the McCollum diet, though lower in the case of calcium and higher for vitamins A and D. On the whole, the self-selected diet was more economical, as measured by dry weight and caloric value, than the artificial one. The question as to how the rat succeeds in making advantageous use of the food constituents at its disposal, taking just as much of each as is necessary, is at present not fully solved, but it seems most likely that it has a specific appetite for each which is satisfied when the needed amount is ingested. Just as lack of food, signalled by hunger, or lack of water, signalled by thirst, lead to an appetite for food or water, and a high valence of these things, so it appears probable that lack of salt, or of vitamin B₁ for instance, induces a specific appetite for these substances, signalled possibly by some change in the smell and taste receptors, whereby the taste or smell of these substances becomes attractive, and remains attractive until such time as the deficiency is made up. It has, for instance, been shown by Richter (1936*a*) that adrenalectomised rats have a greatly increased salt need, which is accompanied by a greatly increased appetite for sodium chloride and the ingestion of about six times the amount taken by normal rats, whose lower salt consumption corresponds closely to their needs. They also show an increased appetite for sodium lactate and sodium phosphate, and rats allowed to choose freely from a range of mineral solutions select these substances (together with sodium chloride), and show a

nearly complete recovery from the normally fatal results of adrenalectomy (Richter and Eckert, 1938). The two ways in which this choice might be effected are balanced against one another in the following passage: 'It is not possible at present to state whether the ability of the rat to make beneficial selections of minerals depends upon experience or on more deeply lying biological factors concerned with chemical changes in the taste and smell mechanisms. It may be that the animal learns to associate relief from deficiency symptoms with the ingestion of certain minerals and not with others; or it is possible that glandular disturbances produce chemical changes particularly in the taste apparatus, which result in making certain minerals much more desirable or pleasant, quite independently of any experience' (p. 222). Evidence in favour of the former alternative has been adduced by Harris and his collaborators (1933) in experiments on rats deficient in vitamin B. If rats are given a diet containing no vitamin B, their appetite begins to drop after about a week and they lose weight rapidly. When a diet containing the vitamin is supplied there is a very rapid recovery of tone and appetite, an increased heart beat, and the rats put on weight. Harris found that depleted rats, given a choice of three foods, only one of which contained vitamin B, very rapidly selected that food and neglected the others. Given a wider choice of foods, the rat may not discover the vitamin-containing one, but if it does it will stick to it and eat no other. Harris considered that the choice is made through experience of the immediate benefits resulting from consumption of the vitamin-containing food—the stimulating effect, the feeling of well-being which rapidly results. This is associated directly with the smell and taste of that particular food, which therefore continues to be chosen.

In the particular conditions of his experiments Harris's conclusion may be valid, but as Richter, Holt and Barelare (1938) point out, it hardly seems to fit their experiments on self-selection of an adequate diet by rats, where the effects of eating any substance do not usually appear for many hours or even days. 'The fact that all of the rats made essentially the same choices, and without any apparent experimentation, indicates that some other mechanism must be involved' (p. 743). 'It would seem more likely', they continue, 'that nutritive deficits produce physicochemical changes throughout the entire body, including the taste mechanisms in the mouth, and that these changes may entirely alter the taste for different substances. In response to these changes an animal may be stimulated to seek certain substances in much the same way as dehydrated animals are stimulated by a dry throat to seek water.' The same authors (1937) have also demonstrated the remarkable fact that vitamin B₁ in pure solution exercises an irresistible attraction for rats deficient in that vitamin, and also for normal rats. Both the smell and the taste of the solution excite a craving for it. It appears therefore to be both attractive and satisfying, *before* any experience of its beneficial results, which appear later.

The question has been discussed at some length by Katz (1937), who comes to the conclusion that choice of food and the specific substances required for metabolism depends essentially upon specific appetites, closely related with biochemical changes, and only to a minor extent upon experience and association. It is not necessary for our limited purpose here, which is to demonstrate the directiveness of behaviour in satisfying needs, to attempt to decide between the two views. The essential thing from our point of view is that need for a particular substance sets in train

behavioural activities that are directive towards satisfying that need, and cease when the need is supplied.

One further example of behavioural action directive towards satisfying a metabolic need. The red deer (*Cervus elaphus scoticus*) of the Western Highlands of Scotland live for the most part in areas deficient in lime, and show a specific appetite for any substances containing calcium and phosphorus (Darling, 1937). This is especially noticeable when the stags are growing their antlers, when the need for these bone-building substances is particularly acute. Darling has observed that they will eat the 'velvet' as it strips off from their own and others' antlers, and that when the antlers are shed they will eat them from the points downwards till only the butt is left. The deer will also chew up the dry skeletons of their kind, first the ribs, then the long bones and the front part of the skull. Stags are avid for the new grass on burnt ground, on account of its high ash content, and they have even been seen to feed on dead frogs. As Darling puts it: 'The stag, craving minerals when growing his new antlers, becomes quite resourceful in trying to satisfy his appetite for lime, and ready to become carnivorous for the moment' (p. 7).

Finally, it is worth while noting that substances may be ingested that are not directly used in metabolism, have no nutritive function, but yet are required for the purpose of digestion; a familiar example is the swallowing of sand and tiny stones by geese and other birds, which are held in the gizzard to assist in the grinding of the food.

4. CONCLUSIONS

The examples we have given of the satisfaction of metabolic needs through behavioural, physiological and morphoplastic activities, which are functionally equivalent and complementary to one another, fall conveniently under

the general formula, $BS \rightarrow A \rightarrow ES$, where BS stands for a state of deficiency relative to functional requirements and ES for a state of adequate supply. The SS may be a 'sign' stimulus, as when a slight excess of carbon dioxide beyond normal leads to the physiological regulation of respiration, or it may be a feeling or sensation, as, for instance, thirst or hunger, which leads to behavioural action directive towards supplying the need for food or water.

The general law that emerges may be formulated thus: *If in a living animal any substance necessary for metabolic activity is in deficient supply, behavioural, physiological or morphoplastic activities, or a combination of them, will normally be set in train that are directive towards remedying the deficiency.* This resembles, of course, the law of the restoration of norms which we formulated above (p. 44), and many of the characteristics of directive activity which we noted in connection with the restoration of norms appear also in the satisfaction of needs.

In concluding this section, let me try to make clear just how the point of view of functional biology differs from the more usual standpoint of mechanistic or causal analytical biology.

From the functional point of view, we are not concerned primarily with the 'mechanism' or exact mode of operation of the responses we study. We are interested primarily in the function, or biological significance of these responses, in the SS or the need that elicits them, in the conditions in which they arise, are continued and cease, in their relatedness to other activities of the organism and to one or other of the main biological ends. In considering, for example, the behaviour of the tissue cells concerned in wound-healing, or the action of the cells of *Microstoma* in transporting nematocysts, it is not of great importance, from the functional point of view, to know the exact mechanism of their movements, though this is, of course,

a perfectly legitimate subject for study. The facts can be formulated and understood biologically without reference to the mechanism of the actions involved, and the functional interpretation is clearly essential for the understanding of the facts; it forms in fact the necessary basis or background for any subsequent endeavour to work out the exact mechanism of the actions under investigation. It is to be noted, too, that the adoption of the functional point of view does not preclude, but often requires, the use of exact physical and chemical *methods* in the effort to discover the way in which organic activities contribute to the reaching of biological ends. Little progress, for example, could have been made in the study of respiration, or of the constancy (homeostasis) of the *milieu interne*, without the use of refined physical and chemical technique. Yet, as the work of J. S. Haldane and W. B. Cannon clearly shows, the use of this technique is quite compatible with a functional and biological point of view, and is indeed necessary for the full elucidation of the functional relations involved.

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RELATION OF GOALS TO
BIOLOGICAL ENDS

1. Having demonstrated, I hope, the existence and importance of directive activity in the restoration of norms and the satisfaction of needs, through behavioural, morpho-plastic and physiological means, which are functionally equivalent, I shall attempt to state and exemplify in this and the next section certain general characteristics or laws of directive activity which seem to me significant, expanding the preliminary discussion undertaken in the previous section. I make no hypothesis as to the nature or philosophical ground of directiveness; I accept it as a fact.

The first generalisation I put forward is as follows:

The goal of a directive action or series of actions is normally related to one or other of the main biological ends of maintenance, development and reproduction.

The goal or terminus of action is, of course, to be distinguished from the biological end which it subserves; this I think I have made sufficiently clear already. The goal of wound-healing is the restoration of continuity and normality of structure in the superficial tissues which have been injured; when this is achieved the directive actions involved come to an end or terminus. But the covering over of the wound clearly helps towards maintenance or survival, and this is the biological end which is served by the goal-directed actions of wound-healing. It is not

implied by the use of the word 'goal' that the agents concerned are conscious of it before it is reached; their action is directive, but not purposive.

That the directive activities which we have studied hitherto help towards the maintenance of the functional integrity and active existence of the individual organism needs no demonstration; that is clearly their biological function and significance. Goal-directed activity related to self-maintenance comes, as we have seen, under the general formula $BS \rightarrow A \rightarrow ES$, where BS represents a state of need or deviation from normality and ES the state of satisfaction of need or restoration of normality. Activities related to the biological ends of reproduction and development present a different form. They are parts or constituents of an organised complex of behavioural, morphogenetic and physiological activities which proceed from a simple or undifferentiated beginning to an elaborately organised end-state, sometimes followed by regression to a less differentiated state. They are characterised by continuous progression towards a future state, which is specific and definite; there is not simply a restoration of normal relations, as in the goal-directed activities of self-maintenance. It is in fact in development and reproduction that the forwardly directed nature of organic activity is most clearly shown.

I shall try to illustrate this by considering first some examples of goal-directed activities related to reproduction.

2. One very general and widespread feature of the reproductive process is the provision in various ways of food for eggs and young. Many animal eggs are provided with a store of nutritive material or yolk, which serves the metabolic needs of the developing embryo or larva and is gradually used up for this purpose as development proceeds. The amount may be very small, as in the egg of *Echinus*

or *Ostrea*, where the larva quickly begins to feed itself, or it may be very large, as in the ovum of the dog-fish (*Scyliorhinus*), which takes about 7 months to develop and hatch, during which time it is nourished solely by the yolk.

The ovum acquires this material in various ways. In *Hydra* one of the developing eggs—a group of well-nourished interstitial cells—takes the lead over its fellows and actually ingests and feeds upon them, obtaining thus a store of nourishment which it lays down as yolk granules. More often there is structural and physiological provision made in the ovary by the formation of follicle and nurse cells which transfer food material to the ripening egg. This is seen very clearly in many insects; in some groups, with ‘telotrophic’ ovaries, the nurse cells clustered at the apex of the egg tubes are connected with the ripening eggs farther down the tubes by means of long nutritive cords through which transfer of food material is effected.

Where the ovaries reach a large size at the breeding season, as is the case in many teleostean fish, their growth and stocking with yolk puts a heavy strain on the somatic tissues, which yield up protein and fatty substances to the gonad. In the herring of the southern North Sea, for example, there is a limited period of intensive feeding in the spring and early summer on a rich planktonic diet, with the result that stores of fat are laid down in the liver, in the mesenteries round the intestine and in the muscles. When feeding stops, the growth and ripening of the gonads begin, and they grow first at the expense of the liver fats, then of the mesenterial reserves; the muscle stores are not drawn upon till the last stages of ripening. In the salmon, the growth of the gonads takes place mainly at the expense of the muscles, which yield up to them fat, protein and inorganic phosphates. ‘From these substances the ovaries build up their essential constituents—the phosphoprotein

ichthulin and the phosphorised fats' (Marshall, 1922, p. 292). Before it runs up its river to spawn, the salmon has accumulated rich stores of fat and other materials in its muscles, and during the period of ripening of the gonads, which may be spread over several months of river life, it takes no food. During this period the needs of the gonads prevail over the needs of the somatic tissues, and by the time the eggs are fully ripened and spawning is imminent the fish is very thin and out of condition.

There is no need to go into details about the formation of yolk and the source of it; the directive nature of the process is obvious. It is also proleptic or anticipatory, in the sense that it provides for the *future* needs of the developing egg.

The provision of yolk is, of course, a physiological and morphogenetic activity, as is also the formation of egg envelopes. Now it is very interesting and significant that the same result—the provision of food for future development—can be reached through the instinctive behaviour of the parent animals. Examples are many. Most of the scarabeids or dung beetles amass and bury stores of dung sufficient to provide for the complete development and metamorphosis of their offspring. Here is the outline of the story so far as it concerns *Scarabaeus sacer*. This is the famous scarab that can be seen on hot days in the south trundling its ball along to bury it in the ground. It does this for one of two ends, either to consume the dung for its own nourishment or to construct with it a pear-shaped mass in which it lays an egg. For the first end, any kind of dung will do; for the second it selects, according to Fabre, a soft mass of sheep dung. Either it buries this on the spot or rolls it away to a place more suitable for excavation, digging a vertical tunnel about 10 cm. deep, then a horizontal gallery ending in a chamber about the

size of one's fist. There it models the dung into a spherical shape, kneading the outside of it so that it forms a hardened crust. At one point it makes a small cavity surrounded by a raised lip; here it deposits the egg, closing it in by extending the circular lip upwards and inwards so as to form a closed cone. The mass thus acquires its pyriform shape, with the egg enclosed in a small air space at the narrow end (Fig. 5). When the larva is hatched it begins to devour the dung, which is kept moist inside the hardened cortex and is further protected from desiccation by being buried in the ground. It eats out the dung from the inside, and is able to repair with its own excrement any breaches made in the wall of the 'pear'. Larval life lasts some 4-5 weeks, and is followed by metamorphosis, also inside the pear. The fully formed beetle is ready for exit usually by August, and by this time the pear is dry and hard, and the scarab must await the autumn rains soaking into the soil and moistening the pear before it can escape. As Fabre remarked, the pear is curiously analogous to the heavily yolked egg of a bird, having a hardened crust or shell, and containing an adequate supply of food material for the developing being as well as an air space. Its formation is due entirely to pure instinctive behaviour, which is directive towards its goal or terminus.

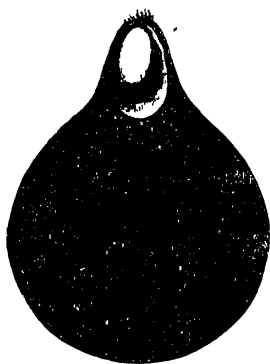


Fig. 5

Another example of the instinctive provision of food for offspring which the parents never see is supplied by the hunting wasps such as the Sphegidae, Pompilidae and many others, which collect and paralyse caterpillars,

spiders and so on, stowing them in burrows or cells, and laying an egg on or close to them, so that when the larva hatches out it has ready to hand a store of fresh food on which to batten.

Then there is the case of the parasitic Hymenoptera, which insert their eggs into suitable insect hosts at the expense of whose tissues the larvae develop. Here perhaps we can hardly speak of the collection and provision of food, though the action of the ovipositing female does in effect secure for her offspring an adequate supply of meat convenient to them. So, too, in the numerous cases where insects lay their eggs on particular substances, such as carrion or dung or on specific food plants serving for the nutrition and development of their larvae, they are in effect providing a supply of food.

In mammals the nourishment of the intra-uterine embryo is secured by the placenta, and during pregnancy the mammary glands grow and develop in such a way that they are ready to produce milk when birth takes place. The valent stimulus for the development of the milk glands is a secretion from the corpus luteum. This provision of suitable food at the right time by morphogenetic and physiological means is followed up by a behavioural utilisation of it, in which mother and offspring commonly collaborate. The pup instinctively seeks the teat; the bitch lies down and offers her stores, often nuzzling the pups into position. Later on she feeds them with regularity, until in the end she forcibly weans them. It is an interesting fact, well known to dog breeders, that some bitches towards the end of the lactation period will disgorge for their pups food which they have recently swallowed; here the physiological provision is supplemented through special behavioural action. Disgorgement may be followed up by the bringing of recently killed food for the young, as is the rule with

carnivores in the wild, and common with the domestic cat.

In birds the provision of food for eggs and young is ensured in several functionally equivalent and complementary ways. Before hatching, the developing bird is nourished by the yolk accumulated in the egg by physiological and morphogenetic activities which have taken place in the body of the mother. In nidifugous types, with their large eggs, the amount of yolk is so great as to enable the young birds to hatch out in a fully fledged state; they may even be capable of feeding and fending for themselves without any help from the parent birds, as is the case with the megapodes. More usually the newly hatched young of nidifugous types require some little help from their parents in the finding and picking up of their food. In nidicolous kinds, on the other hand, the nestling is completely dependent upon the food brought to it by its parents and often delivered directly into its mouth. The instinctive behaviour of the nestling plays an indispensable part in this feeding process; the passerine nestling, for instance, raises its head and gapes widely for the food about to be received, and if it did not show this response it would not be fed. In some groups semi-digested food is regurgitated for the young to pick up, or it may be held in the throat from which the young pick it out. In pigeons a kind of 'milk' is produced by the fatty degeneration of the epithelial lining of the crop, and regurgitated for the nourishment of the early squabs.

These various methods of ensuring a food supply to the developing young are complementary to one another, and directive towards the same end or result. The supply of yolk in nidicolous forms, which is insufficient for development to a self-feeding stage, is immediately supplemented, on hatching, by the food brought in by the parents and

accepted actively by the young. Instinctive behaviour by both parent and young here continues the work of providing food which was begun by the physiological and cellular activities concerned in the accumulation of yolk in the egg, and is functionally equivalent to these activities. None of them is of course consciously purposive, but all might be called instinctive. When later the young bird becomes independent of parental help it depends upon its own instinctive equipment for the finding and intake of food.

It is characteristic of the reproductive cycle, especially in highly organised forms like the vertebrates, that the physiological, morphogenetic and behavioural activities concerned are very closely correlated with one another, and co-operate smoothly towards achieving the biological end of successful reproduction—and all without foresight or forethought. I have called attention to this feature of the reproductive cycle in previous publications (Russell, 1934, pp. 7–8, 122–9, and 1937*a*, pp. 72–5), and it is unnecessary to illustrate it in detail here. But I may be allowed to quote the following passage in general illustration: ‘In the reproductive cycle of birds we see very clearly the interweaving of instinctive behaviour with morphogenetic and physiological changes. Many birds migrate towards their breeding areas as the days begin to lengthen and their ovaries and testes to wax in size. Sometimes the male arrives first and chooses a territory, from which he wards off intruders and to which he attracts a mate. Courtship follows, and, when both male and female have reached the right state, insemination. Nest building has also begun, and normally when the nest is ready, and not before, the first egg is laid. Now the laying of the egg is the end-result of a long organic preparation; germ-cells are formed at a very early stage of development, an ovary and an oviduct also. These grow and mature,

reaching full development as the breeding season culminates. The egg is supplied with its yolk, its albumen, its shell, and is ready to be laid when the cycle of behaviour has produced the nest. We should not, indeed we cannot, separate instinctive behaviour from morphogenesis; both are essential and interrelated parts of the one unitary cycle.

'We see the same thing in the reproductive cycle of mammals. As pregnancy progresses, there is a preparation, both organic and behavioural, for the care of the coming young. The mammary glands enlarge before, and become actively functional immediately after, parturition; the mother often prepares a bed or nest just before she is ready to give birth. She gives suck to her young, keeps them warm, often retrieves them when they stray from the lair. As time goes on, the maternal instinct dwindles in intensity, the mammary glands regress, and the "valence" of the young sinks to zero' (1937*a*, pp. 73-4).

One further example may be given of the functional relatedness of physiological, morphogenetic and behavioural activities to the biological end of reproduction, and their correlation *inter se*, and for this purpose I select the fascinating story of the laying of eggs and their attachment to the abdominal appendages in decapod Crustacea, as worked out by Yonge (1938) especially for the lobster (*Homarus vulgaris*). These are essential steps in the process of reproduction, for without proper attachment the eggs would certainly not survive. Through the directive activities of development the abdomen of the female is pre-adapted for the reception, attachment and protection of the eggs. It is broader than in the male; the pleural plates walling it at the sides are considerably larger, and are fringed by 'a much denser layer of setae which are some three times longer than those of a male of similar size'. The last four pairs of pleopods are considerably

larger in the female (Fig. 6, left), and, in addition to the dense fringe of plumose swimming setae (*s*) which are common to male and female, they are provided with tufts of long, non-plumose setae (1-7) which are completely absent in the male. These serve exclusively for the attachment of the eggs, none being fixed to the plumose setae except adventitiously.

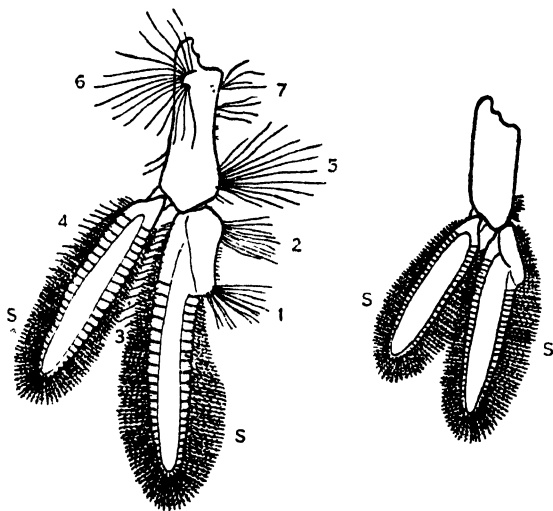


Fig. 6

Yonge has shown that the attached egg has two membranes, the inner a thin chitinous covering closely adherent to the surface of the egg. This is formed in the oviduct as the ripe egg passes down, by secretion from the oviducal epithelium. Just prior to the discharge of the eggs from the ovary, secretion granules accumulate in the distal ends of the epithelial cells, ready to provide the membrane, and after this is done the cells regress to a resting state.

The outer membrane is composed of cuticular substance which is continuous with the twisted strands of similar composition that attach the eggs to the non-plumose setae. This substance is formed in, and discharged from, the cement glands that occur in profusion in the pleopods of the female, through long ducts that open on the edges of the non-plumose setae. These glands are indistinguishable from the tegumental glands which occur everywhere under the chitinous epithelium and form the general cuticle. Like the chitin-secreting cells in the oviduct, they are active only at the time when the eggs are being laid. Their activity is therefore correlated with egg-laying, whereas that of the tegumental glands is correlated with moulting, immediately previous to which they actively secrete cuticle. The biological function or significance of the secretion process is different in the two cases. It is of interest that in the male there are only a few scattered tegumental glands in the pleopods, sufficient for cuticle formation; it lacks the great development of cement glands which is required in the female for the attachment of the eggs.

It is well known that in decapod Crustacea reproduction is closely associated with ecdysis. 'Copulation follows ecdysis, the reception of the spermatophores by the female appears eventually to induce ovulation with which are associated the secretion of chitin by the oviducal epithelium and, probably simultaneously, secretion by the cement glands. The sexual cycle is thus intimately associated with ecdysis, mating being usually only possible immediately after this, while the processes involved in the formation of the two egg membranes are both of them modifications of those involved in ecdysis' (p. 513). Cuticular substance is peculiarly well suited for the attachment of the eggs to the pleopods. In fact, 'the attachment of eggs in *Homarus* and allied Decapoda re-

presents the exploitation of a substance which forms the outer covering of the integument and the properties of which—low surface tension, slow modification in water, final hardness, and limited permeability—combine to make it ideal for both purposes' (p. 513).

So much for the morphogenetic and physiological activities which contribute to the attachment of the eggs; it is noteworthy how accurately timed and adjusted they are to the needs of the situation. (It is probable, as Yonge points out, that some of them are under hormonal 'control', a hormone acting, for instance, as the adequate stimulus for glandular activity; if this be so, it does not by itself account for the timing, for the question inevitably arises why the hormone is produced just at the right time, or alternatively why the glands are tuned to respond to it at the appropriate moment.)

Following on these physiological activities preparatory to attachment the behaviour of the female plays an indispensable part. Yonge quotes from Andrew Scott the following description of the behavioural activities of the lobster during the laying and attachment of the eggs. 'The lobster turns on to its back and by the aid of the two large claws and ridge of the abdomen makes a tripod of itself, the head being considerably higher than the posterior portion. The abdomen is then strongly flexed, forming a pocket, and the setae on the edge of the abdominal segments make the space along the sides perfectly tight. A Λ -shaped opening into the pocket is formed by the telson and the sixth abdominal segment. This opening, when the abdomen is flexed, is slightly posterior to the first pair of swimmerets. The eggs then flow from the two genital openings in a continuous stream, one at a time, and pass along at the bases of the last walking legs and into the opening of the "pocket". The course of the eggs into the

"pocket" is further assisted by a constant pulsation of the first pair of swimmerets, causing an indraught, which carries them inside. None of the eggs is lost on the passage from the genital openings to the "pocket" unless the lobster is disturbed' (p. 502).

Looking back, we see that the attachment of the eggs to the pleopods, which is a goal subordinate to the biological end of reproduction, involves a complex of activities of different kinds including behaviour, all directive towards this goal and closely co-ordinated in time. It is impossible to understand them if we do not recognise their directive-ness, and their functional relation to the goal. Yonge himself uses, quite rightly, the words 'function', 'need', and 'purpose' in his description of events, and, as we have seen, emphasises the relation of the secretion of chitin and cuticular substances to the immediate goal of action, which is either egg-laying and attachment, or the formation of a new integument in ecdysis.

In the shrimp (*Crangon vulgaris*, and in others of its family) the egg-carrying setae are very small, and cement glands are absent, in the immature female; prior to the moult that marks the change-over to maturity, the ovary develops rapidly, and after this moult the egg-carrying setae appear in full size, accompanied by cement glands. Pairing and spawning then normally take place, and after the eggs have been shed the female moults into a 'neuter' condition, with setae reduced and cement glands absent. 'The ovary then increases in size, and in due course the animal moults into the egg-carrying condition with both spines and cement glands. This alternation of "neuter" and egg-carrying conditions apparently continues throughout the remainder of the life of each female' (Lloyd and Yonge, 1940). In this remarkable case, setae and cement glands are formed anew, as the need for them arises.

3. It is not necessary to illustrate in any great detail the obvious fact that the activities concerned in development are directive towards the reaching of specific and normal end-states or termini, and culminate in the reconstitution of the complete adult organisation typical for the species; they can be understood by us only if their relation to the biological end of self-completion is known and held in mind. Developmental processes, objectively considered, are aimed at the future, they are directive, one might say, towards supplying future structural and functional needs. The characteristic and remarkable feature of developmental processes is precisely their proleptic or anticipatory nature, their prospective reference, their building for the future. This may be evident, even in the early stages of cleavage, as E. B. Wilson has pointed out. 'Analysis of the cell-lineage of annelids and mollusks', he writes, 'led F. R. Lillie to the conclusion that in many cases the rate of cleavage obviously shows a direct relation to the period at which the products become functional and the number of cells required at this time. In *Unio*, for example, a certain large cell of the second quartet formed at the fourth cleavage shows individually an accelerated division-rate that is correlated with the early formation of the shell-gland to which it gives rise, and with the large number of its component cells; conversely, the relatively slow division-rate of the first quartet of ectomeres is correlated with the reduced condition and small number of cells of the pre-trochal region formed from it. The prospective character of cleavage, here clearly evident, applies to many other of the blastomeres' (1925, p. 997). While many of the cell divisions in early development appear to occur in accordance with simple physical laws, others do not so conform, but show clear reference to the future destiny of the products of division. The teloblasts

which play an important part in the early development of annelids and molluscs divide always unequally and in the same plane, in correlation with the apical growth of the embryo; the apical cells of plants also divide with reference to what is to come. In such cases, 'the simpler mechanical factors, such as pressure, form and the like, are subordinate to more subtle and complex operations involved in the general development of the organism. . . . In all such cases we cannot comprehend the specific forms of cleavage without reference to the end-result of the formative process; and the problems here encountered cannot be separated from those of development in the larger sense. The "teleological" aspect of cleavage thus suggested has been recognised more or less clearly, by many observers; most adequately perhaps by Lillie, who has urged that with this principle in mind "one can thus go over every detail of the cleavage, and knowing the fate of the cells, can explain all the irregularities and peculiarities displayed". The egg is not merely a cell dividing as best it may, under the stress of simple and obviously mechanical conditions. It is "a builder which lays one stone here, another there, each of which is placed with reference to future development". Of the truth of this anyone must, I think, be convinced who has critically studied these phenomena' (p. 1005). Wilson adds to this important passage, with its significant recognition of the need for considering ends for our own understanding of these phenomena, the remark that no mystical doctrine of teleology or final causes need be involved. We may agree, but without committing ourselves to the mechanistic alternative suggested by Wilson, that all is dependent in the last resort upon the organisation or material configuration of the egg. For the moment we are only concerned with the objective fact that these forms of cleavage are directive

towards future goals integrally related to the general process of development, and comprehensible only on this basis, whatever their causal explanation, if any, may be.

One further example may be given of cell division, in apparent contradiction with physical laws, which is directive towards a future structural and functional goal, the well-known case of the longitudinal division of the cambium cells in the development and growth of the higher plants. Of this I. F. Lewis writes, following the investigations of Bailey: 'In the white pine the dimensions of these cells have been given as 4000 by 42 by 12 micra. Division planes along the short axis would be confidently expected by the cytologist. Actually division is in the plane least to be considered possible, and the long thin sheet-like cell is split into two still thinner sheets of the same length and breadth. In this unusual behaviour, which in its defiance of physical laws is almost like making water run up hill, the cambium cell, of course, is reacting to some stimulus the nature of which is entirely obscure. The result, however, is a happy one, producing the very long cells needed in the conducting system of the stem' (1940, p. 99). Much of early development appears to us as a preparation of structure for future functioning. As W. Roux pointed out many years ago (in 1881), there can be distinguished in development two stages or periods, first a period of self-differentiation of structure in which the organs are roughed out in readiness for functioning, and a period of functional development in which the organs are perfected through functioning (details in Russell, 1930). In vertebrates with a long embryonic life, protected from outside influences, in birds and mammals for instance, the first period is the more important (and even after birth maturation plays a great part in what appears to be active learning). Much of the adaptive

structure of the bones, for example, is developed long before the embryo can use its limbs (Murray, 1936; see Fig. 23 on p. 167 below). In regeneration also, morphogenetic or morphoplastic activity precedes and prepares for the resumption of normal functioning. This feature of development and regeneration has been vividly illustrated by Sherrington in the following passage: 'The regenerating nerve rebuilds to a plan that spells for future function. But throughout all its steps prior to the actual reaching the muscle or skin no actual performance of nerve-function can take place. What is constructed is functionally useless until the whole is complete. So, similarly, with much of the construction of the embryo in the womb for purposes of a different life after emergence from the womb; with the construction of the butterfly's wing within the chrysalis for future flight; of the lung for air-breathing after birth; of the reflex contraction in the foetal child of the eyelids to protect the eye long before the two eyelids have separated, let alone ere hurt or even light can reach it. The nervous system in its repair, as in its original growth, shows us a mechanism working through phases of non-functioning preparation in order to forestall and meet a future function' (1922, p. 8). The development of structure in complete independence of functioning is strikingly illustrated in the phenomena of insect metamorphosis. In the more complete types of metamorphosis there is 'a doubling of most of the rudiments of the organs in the embryo. On hatching, one set of these rudiments develops immediately into the larval body, while the other set remains in abeyance in the form of minute germinal centres, or histoblasts, from which the body of the adult will be fashioned during the quiescent pupal stage' (Wheeler, 1928, p. 60).

In development, morphogenetic activities are, of course, those mainly concerned—the directive growth and dif-

ferentiation of cells, and their arrangement to form tissues and organs. But the active movements and behaviour of cells also play an important part, as is evident in the formation of bones in vertebrates, and very clearly so in the formation of spicules in sponges (see Section VI, pp. 159-65). So, too, the behaviour of the developing animal itself may be an essential factor in achieving successful development. Many animals require for successful development a particular set of environmental conditions, and the finding of this ecological norm may be dependent on the instinctive behaviour of the larvae or young.

Like other animals that live buried in the sea bottom (see Davis, 1925), many polychaete worms are restricted to a particular grade of material, in which alone they are found. The pioneer work of Wilson (1932) indicates that in some cases at least the proper substratum, suitable for the life of the species, is found by the pelagic larva. This is so with *Owenia fusiformis*, the mitraria larva of which is normally pelagic for some 4 weeks, during which time it swims strongly, with an upward tendency. After this period, when ready to metamorphose, it sinks towards the bottom and swims slowly along in contact with it. If the bottom is of fine sand or grit, similar to that in which the adult worm lives, the larva responds to the specific contact-stimulus by settling down, metamorphosing into the tiny worm and building a tube with the aid of mucus. As a rule it will not metamorphose on any other kind of bottom, as for instance fine mud or a clean glass surface, but will retain its pelagic habit and structure for an abnormally long time. It may, however, ultimately metamorphose, usually in an abnormal manner, on such a bottom; Wilson found, for example, that if kept for a long time in a glass dish containing the small diatom *Nitzschia* and some fine dust the larvae made shift to metamorphose, but only three out

of fourteen metamorphosed in a normal way and formed mucus tubes with the dust and the *Nitzschia*.

The larvae of *Scolecoplepis* behave in a similar way (Day and Wilson, 1934). They metamorphose readily on a bottom of muddy sand, the ecological norm of the species being somewhat different from that of *Owenia*. Kept in vessels with a substratum of glass, or mud, or 'silver sand', they delay their metamorphosis up to several weeks, but in the long run an attempt is made at metamorphosis, which may or may not result in a normal worm. Day and Wilson noted that 'in all cases the larvae explored the vessel, crawling over the bottom and attempting to burrow. If the bottom proved suitable they metamorphosed, otherwise they alternately burrowed and swam' (p. 656). Similar results were obtained with the larvae of *Notomastus* (Wilson, 1937).

In a previous paper (1928) Wilson describes how the larvae of *Polydora* crawl over oyster shells (in which the worm lives, in little burrows) exploring every small hole and crevice they come across, and creeping in between the layers of the periostracum, finally settling in a suitable crack. In all these cases the development of the worm could not be successfully accomplished without the effective behaviour of the larva in occupying the environmental niche to which the species is pre-adapted. I have elsewhere given several other examples of this co-operation of behavioural with developmental activities in relation to the ecological norm (Russell, 1934, 1941), and need perhaps refer to only one more. The cicadas lay their eggs in the tissues of plants, either in the twigs and branches of bushes and trees or in the stems of herbs and grasses. This is not the ecological norm in which the larvae or nymphs develop, for they live and grow underground, in proximity to the roots of trees and other vegetation on which they

feed, but it is a position from which the larvae can reach their ecological norm by their own exertions. They hatch out as tiny sheathed nymphs and climb out of the egg-nest towards the light, moving upwards and outwards to the ends of the twigs; then they let themselves fall to the ground and immediately creep down any crevice that presents itself or actively burrow into the earth. This instinctive behaviour is essential for their subsequent survival, and is correlated with the needs of the developing nymph.

Behaviour takes a hand too in the selecting of a suitable spot for pupation in such insects as undergo complete metamorphosis, in the weaving of a protective cocoon, sometimes with special provision for the easy exit of the imago, in hatching out from the pupal case and in expanding the wings ready for flight; these instinctive activities form a necessary link in the chain of morphogenetic processes which lead to the fulfilment of development.

The functional equivalence of behavioural and physiological activities in achieving or reaching a developmental goal may be illustrated by a couple of examples.

The often elaborate tests or 'shells' of the Foraminifera are in most groups formed by secretion, but in the Astro-rhizidaceae and the Lituolidaceae the tests are arenaceous and formed almost entirely by foreign particles picked up by the protozoan from its surroundings and built into the shape characteristic for the species. In the Lituolidaceae the very diverse forms of test produced by 'building' are isomorphic with the tests of genera, such as *Cornuspira*, *Peneroplis*, *Lagena*, *Globigerina* and others, which are produced by secretion (Hartog, 1906, p. 65); behaviour produces the same result as the physiological process of secretion.

In the arenaceous groups there is an active selection of appropriate building material, which is thus described by

Carpenter: 'From the same sandy bottom one species picks up the coarsest quartz grains, unites them together with a ferruginous cement, and thus constructs a flask-shaped test, having a short neck and a single large orifice; another picks up the finer grains and puts them together with the same cement into perfectly spherical tests of the most extraordinary finish, perforated with numerous small pores disposed at pretty regular intervals. . . . And another, which makes a straight, many-chambered test, the conical mouth of each chamber projecting into the cavity of the next, while forming the walls of its chambers of ordinary sand grains rather loosely held together, shapes the conical mouths of the chambers by firmly cementing together the quartz grains which border it' (quoted by Hartog, 1906, p. 64).

The selection and utilisation of sponge spicules for building purposes is illustrated and discussed by Heron-Allen (1915).

A parallel to this is afforded by the polychaetes, many of which form a permanent tube by selecting material from the sea bottom and building it up in well-knit and characteristic shapes. As Benham points out (1896, p. 287), tube-making is not a simple process, 'for in many cases, at least, the worms exhibit definite powers of choice. Thus some species of *Sabella* choose only the finest particles of mud; *Terebella conchilega* chooses fragments of shell and grains of sand; *Onuphis conchylega* employs small stones more or less of a size; *Sabellaria* makes use only of sand grains. Whilst some worms, like *Terebella*, *Nicomache* and others, make a very irregular tube, *Pectinaria* builds a most remarkable neat house, open at each end, which it carries about with it, the narrow end uppermost; the grains of sand are nearly all of the same size and only one layer in thickness, embedded in abundant "mucus", and with the

outer surface quite smooth'. In other kinds, the tube may be formed entirely by physiological processes of secretion, as in *Hyalinoecia* among the Eunicidae, and notably by the Serpulidae, with their thick calcareous tubes of characteristic shape. The statoliths of Crustacea are formed by secretion in some groups; in others functionally equivalent sand-grains are introduced into the otocysts by the animal's behavioural activity.

The analogy between the repair of its case by the caddis larva *Molanna* and the morphoplastic activities of regeneration has already been noted (p. 22).

In conclusion, one may refer to the curious phenomenon of 'phragmosis', a term introduced by W. M. Wheeler to designate those cases where a specially modified part of the body acts as a plug to stop up a hole or burrow. The soldiers of the ant genus *Colobopsis*, for example, have the front part of their head flattened and so shaped that it fits the nest-hole and acts as a 'living door', to use Buytendijk's apt description (1928, p. 132).

Certain spiders that live in burrows close the entrance not with a lid or a web but with their own hind body, which is abruptly truncated and fits the hole like a cork. The burrowing toad (*Bufo empusus*) (Fig. 7) has a horny head that forms a perfect operculum and accurately fits the calibre of the burrow in which it lives (Barbour, 1934, p. 76). In armadillos of the genus *Chlamydophorus*, which live



Fig. 7

underground in burrows, 'the posterior end of the body is as if sharply chopped off and is covered by a bony shield.

This closes the burrow perfectly and no prying snake following its underground path could possibly get its jaws about it' (Barbour, p. 77). In all such cases an end—the stopping up of a hole or burrow—is achieved by the morphogenetic processes of development, coupled of course with appropriate behaviour, which is more usually attained by behavioural or physiological activities pure and simple. The moral is drawn by Wheeler, as follows: 'The phragmotic insect, instead of constructing a stopper, like the operculum or epiphragm of snails and the earthen or silken barricades erected at the entrances of their burrows by many ants, wasps and trap-door spiders, actually employs for the purpose a specialised portion of its own body, thus affording a proof that no hard and fast line can be drawn between behavioristic activities on the one hand and physiological and morphogenic processes on the other' (1928, p. 42).

4. While the goals reached by directive activity are *normally* related to the biological ends of maintenance, development and reproduction, and directive activity is therefore as a rule biologically purposive, there is no necessary or inevitable connection between directiveness and biological 'purposiveness'; directive activity may lead, especially in abnormal conditions, to biologically unpurposive results. The 'teleology' of vital processes, if one may use the word, is therefore a limited one; there is nothing 'mystical' or miraculous about it; it is a natural phenomenon and subject to natural restrictions.

Instinctive behaviour, for instance, which is a form of directive activity, is adapted to deal with the normal or usual conditions which the animal encounters, and it easily goes astray if the conditions are abnormal. The perceptual signs which are normally adequate to characterise a biologically significant object or event, and to which the

animal is predisposed to attend, may occur by exception in connection with an unsuitable object and lead to action which is biologically unpurposive—as we saw when we considered the instinctive behaviour concerned with food-finding (pp. 63–9); it is not, for instance, a biologically purposive act for a boa to strike at a warm, moving electric bulb as it would at a living prey, nor for a scarab to trundle away a chestnut smeared with dung. Instinctive behaviour is easily misled. The instinctive animal is also wedded to a fixed routine of action, adapted to normal situations and normal sequences, a routine which it may not be able to alter to fit the altered circumstances; in such case, its actions, though goal-directed, become biologically inadequate or non-purposive, they do not contribute to a biological end.

I have dealt with this well-known stereotypy of instinctive behaviour in previous papers (1937*b*, 1944), from which I take the following examples. In most species of pigeon, according to Lorenz (1935), the female sits on the nest from late afternoon till the next forenoon, the male during the rest of the day. If the female is killed the male continues his routine of incubation, but makes no attempt to extend it to replace the missing female. Here is a case described by Lorenz (1935, p. 343). A pair of house pigeons had hatched out their nestlings when the female was taken by a cat. The male sat on the nest during his normal period for incubation, and shortly after the hour when he would have been relieved by the female had she been alive he went off to feed. In the evening he took up his usual sleeping perch near the nest, leaving the nest uncovered, and as the night was cold the nestlings perished. In the morning, about ten o'clock, the male settled down on the nest and brooded the little corpses till late in the afternoon, when he went off to feed and sleep. He kept up this sense-

less routine for two days, being unable to break or modify it. Similar cases in pigeons and other birds have been recorded from time to time (see Dewar, 1928).

The instinctive actions of a hunting wasp in seeking for prey, stowing it in a burrow, laying an egg on it and closing up the burrow follow one another in a strict routine, which the wasp finds it difficult to break. If the sequence is upset she may behave quite unpurposively. Hingston (1928) relates how the digger-wasp (*Psammophila tydei*) responds, or rather fails to respond, to experimental interference with her routine. She had dug her burrow and provisioned it with a caterpillar on which she had laid an egg, and she was busy closing the burrow with small pebbles and pieces of slate, when Hingston broke open the tunnel and extracted the caterpillar. This he placed right across the entrance to the tunnel. When the wasp returned, she paid no attention to the caterpillar, but went on with her normal routine of closing up the tunnel, a biologically unpurposive act.

Inability to respond effectively to an unusual situation is strikingly shown in the behaviour of the parent bird towards her young that have been jerked out of the nest by a baby cuckoo; she pays no attention to them, and lets them die before her eyes. A case of this kind has been vividly described by Hudson (1903) as follows: 'The young robin, when ejected, fell a distance of but five or six inches, and rested on a broad, bright green leaf, where it was an exceedingly conspicuous object; and when the mother robin was on the nest—and at this time she was on it the greater part of the time—warming that black-skinned, toad-like spurious babe of hers, her bright intelligent eyes were looking full at the other one, just beneath her, which she had grown in her body and had hatched with her warmth, and was her very own. I watched her for hours; watched

her when warming the cuckoo, when she left the nest and when she returned with food and warmed it again, and never once did she pay the least attention to the outcast lying there so close to her. There, on its green leaf, it remained growing colder by degrees, hour after hour, motionless except when it lifted its head as if to receive food, then dropped it again, and then at intervals it twitched its body as if trying to move. During the evening even these slight motions ceased, though the feeblest flame of life was not yet extinguished; but in the morning it was dead and cold and stiff; and just above it, her bright eyes on it, the mother robin sat on the nest as before, warming her cuckoo' (p. 24). Other cases are reported by Dewar (1928). The lack of attention to the ejected nestling may perhaps be mainly due to its not exhibiting the 'begging' action, the raising of the head and gaping widely. According to Tinbergen (1938), if the nestling is replaced in the nest with the young cuckoo, it will not be fed until it warms up and begins to show the gaping reaction.

The behaviour of the bird in incubating and feeding the alien cuckoo nestling is of course itself biologically un-purposive; the bird is predisposed or tuned instinctively to brood and tend objects in the nest that gape; normally these are its own nestlings, but the same routine course of behaviour continues with the alien nestling, which shows the same valent characteristics.

The stereotypy and inadaptability of instinctive behaviour, which leads in unusual circumstances to biologically un-purposive actions, must, of course, not be exaggerated. Adaptive response to changed conditions may also occur, even in highly specialised instinctive types, such as the insects; a balanced account of the situation will be found in Bierens de Haan (1940, pp. 228-52).

Activities which, though goal-directed, do not further a

biological end may be observed in the reproductive cycle. We have already noted the intimate co-ordination of behavioural, physiological and morphoplastic activities in the pregnant mammal, and how they normally co-operate towards the biological end of reproduction. In the not infrequent phenomenon of pseudo-pregnancy, however, many of these activities take place in preparation for the birth of non-existent young. Thus, in the marsupial 'cat' (*Dasyurus*), pseudo-pregnancy 'is accompanied by a series of changes in the reproductive organs and mammary glands essentially similar to those taking place in gestation. The pouch enlarges and the sebaceous, sweat, and mammary glands also hypertrophy as well as the internal organs. At the end of the period the animal has been seen to clean out its pouch for the reception of young, showing that the developmental and cyclical changes of the sexual organs may extend even to the instincts associated with parturition and the nursing of the young, although true pregnancy had not taken place' (Marshall, 1922, p. 36). So, too, the pseudo-pregnant bitch may prepare a bed, and the rabbit in similar case may pluck her fur and make a nest. All these goal-directed activities pursue their course though their normal biological end cannot be attained.

The activities concerned in regeneration are normally directive towards restoring normality of structure, and are usually therefore biologically purposive. But they may lead to non-purposive results. In the address to which we have already referred (1922) Sherrington describes how a severed nerve grows out from its stump and burrows its way towards its original ending in muscle or skin, which normally it reaches. But by misadventure the regenerating fibres of a motor nerve may end in denervated skin instead of in muscle. 'They find the skin-cells whose nerve-fibres have been lost, and on these they bud out twigs, as true

sensory fibres would do. Then, seemingly satisfied by so doing, they desist from further growth. The sense-cells, too, after this misunion, regain their normal features. But this joining of motor nerve-fibre with sense-cell is functionless, and must be so because the directions of functional conduction of the two are incompatible. So, similarly, a regenerating skin-nerve led down to muscle makes its union with muscle instead of skin, though the union is a functional misfit, and cannot subserve function. Marvellous though nerve regeneration be, its mechanism seems blind. Its vehemence is just as great after amputation, when the parts lost can, of course, never be reached. Its blindness is sadly evident in the suffering caused by the useless nerve-sprouts entangled in the scar of a healing or healed limb-stump' (p. 7). The action of the regenerating nerve is goal-directed, but the goal that is reached may subserve no biological end.

In experiments on regeneration, conditions are often established to which the tissues of the animal respond directly, but achieve a biologically unpurposive result. The hinder end of an earthworm severed from the rest of the body may produce at its anterior cut surface a tail and not a head; the head of a planarian cut off just behind the eyes regenerates at its posterior cut surface another head (see Morgan, 1901, Fig. 16); these responses are directive, but not biologically purposive. Double heads or double tails can be produced in many types of animal by appropriate operation, and monstrosities created by transplantation of organs. Fig. 8 shows the curious result obtained in a planarian by making lateral incisions di-

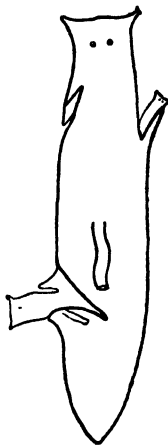


Fig. 8

rected forwards or backwards; a head and part of a body are produced from the backwardly directed cuts, a tail from the forwardly directed one. These formations, though complete in themselves, are of no adaptive or biological value to the planarian; they represent, we might say, the best the tissues can do in the exceptional circumstances created by the experimenter; their action is directive, but not biologically purposive.

It would be easy to multiply cases of biologically useless or even harmful responses to operational interference with regenerative and developmental processes, and to adduce instances of excessive and pathological growths, all showing that directive activity is not necessarily purposive in a biological sense. There is, however, no need to elaborate the theme; nor should we forget the main thing, that directive or goal-directed activities, whether they be behavioural, physiological or morphogenetic, *normally* contribute to the reaching of biological ends. The organism may also adapt its activities to changed conditions, as the facts of functional adaptation so clearly show.

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V

CHARACTERISTICS OF GOAL-DIRECTED ACTIVITY

There are certain general or normal characteristics of all goal-directed activity (whatever its biological end) which may be summarised as follows:

1. When the goal is reached, action ceases; the goal is normally a terminus of action.
2. If the goal is not reached, action usually persists.
3. Such action may be varied:
 - (a) if the goal is not reached by one method, other methods may be employed;
 - (b) where the goal is normally reached by a combination of methods, deficiency of one method may be compensated for by increased use of other methods.
4. The same goal may be reached in different ways, and from different beginnings; the end-state is more constant than the method of reaching it.
5. Goal-directed activity is limited by conditions, but is not determined by them.

I shall now proceed to illustrate and exemplify these rules, which are normally, though not invariably, valid for directive activity, whether behavioural, physiological or morphogenetic.

I. THE GOAL IS A TERMINUS OF ACTION

We have already come across many examples of this well-known fact. When a rat has satisfied its appetite for

a specific food substance it takes no more of it, until the need arises again; a full-fed animal normally ceases to feed. When a wound is healed over and the normal density of cells restored, the cellular activities directive towards these goals come to an end. When *Molanna* has repaired its case to something like normal, it ceases its efforts at restoration. When an animal's normal body temperature is restored by physiological or behavioural action, these regulatory activities are reduced to the minimal level required for the continued maintenance of normality. Here are a few other examples selected at random. When a motor nerve is severed, the fibres that run from the cut to the muscle degenerate and die, but the cut-end at once starts growing out to re-establish connection with the muscle. 'The fibre, so to say, tries to grow out to reach to its old far-distant muscle. There are difficulties in its way. A multitude of non-nervous repair cells growing in the wound spin scar tissue across the new fibre's path. Between these alien cells the new nerve-fibre threads a tortuous way, avoiding and never joining any of them. This obstruction it may take many days to traverse. Then it reaches a region where the sheath-cells of the old dead nerve-fibres lie altered beyond ordinary recognition. But the growing fibre recognises them. Tunnelling through endless chains of them, it arrives finally, after weeks or months, at the wasted muscle-fibres which seem to have been its goal, for it connects with them at once. It pierces their covering membranes and re-forms with their substance junctions of characteristic pattern resembling the original that had died weeks or months before. Then its growth ceases, abruptly, as it began, and the wasted muscle recovers and the lost function is restored' (Sherrington, 1922, p. 6). This is an excellent case of persistent directive action, surmounting difficulties, and coming to an end when the goal is reached. It is, of course,

typical of regenerative processes that they stop when normal structure is restored. If a newt's leg or arm is truncated, the wound is healed and a regeneration bud formed under the new skin. This grows and differentiates, reforming the missing part of the limb, in normal shape. 'When we are dealing with the regeneration of an adult organ such as a newt's limb', writes Waddington (1934, p. 339), 'the equilibrium towards which the regeneration takes place is a stable one; once the whole limb is regenerated, the change stops, except perhaps for growth changes.'

Growth and development in general move towards a definite or end-state, and cease when this is reached. A water-lily leaf grows up towards the surface of the water, and there expands to its full shape; growth persists till this end-state is achieved, and then stops. Pierre Jean, in his remarkable volume on 'organic psychology' (1925), recalls an experiment of Sachs which nicely illustrates the persistence of growth in aquatic plants till the normal position is reached. It is shown in Fig. 9, and needs no explanation.

In animal behaviour cessation of action when the goal is reached is so common a phenomenon as to require no elaborate demonstration. When a starfish or a beetle is turned on its back, the righting behaviour which follows ceases as soon as the normal position is regained.

It is interesting and significant to observe that if the goal or end-state is supplied by external agency, and not by the animal's own efforts, the restorative action will likewise come to an end. If, when the beetle is struggling to right itself, you present it with something to which it can cling, it will cease its efforts, which have now become unnecessary. The same is true of the starfish (see, for instance, Russell, 1919). Something of the same kind may take place in wound-healing; it appears from an experiment of Carrel,

reported by Lecomte du Noüy (1936, p. 98), that the healing activities may cease if the end-state is artificially established by the close application of a piece of cellophane to the wound; effective covering having been supplied, there is no need for epithelisation, and it does not take place.

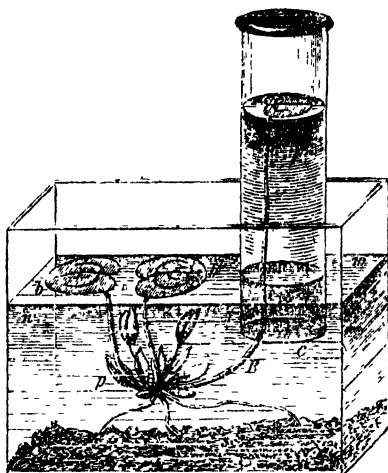


Fig. 9

Here is a more complex but very instructive example, which I take from Boycott (1929). The number of erythrocytes in the mammalian blood—which Boycott calls collectively ‘the erythron’—is kept at a normal level (which is relative to the pressure of the atmospheric oxygen, see p. 28). If the erythron is reduced by severe haemorrhage, the loss is ultimately made good by the production of new erythrocytes from the bone-marrow, a process which goes on till the goal or end-state of a normal concentration is reached. The erythron can also be in-

creased by transfusing an extra quantity of blood into the circulation; when this happens the excess quantity is actively destroyed by phagocytosis and normality again restored. The end-state or goal of these processes is quite definite—the restoration of the normal amount of red cells. Both processes, by the way, are accelerated by practice. Now if, in a bled rabbit, the amount of blood removed is quickly restored by transfusion, and the normal end-state

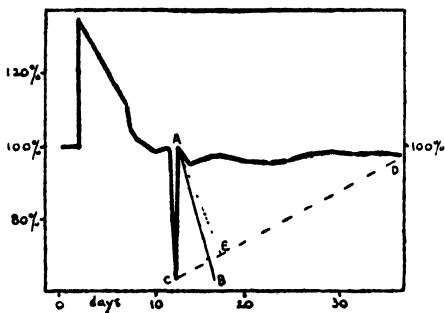


Fig. 10

thus artificially restored, then neither the process of destruction of the introduced erythrocytes takes place, nor the production of new erythrocytes from the marrow, for the goal aimed at has already been reached.

This experiment is best described in Boycott's own words, which are admirably succinct. His diagram is also reproduced here (Fig. 10). 'A rabbit trained by repeated transfusions (the last of which is shown) to dispose of excess blood quickly is bled about a third, and the quantity of erythron removed is immediately replaced from other rabbits. If this last transfusion were destroyed like its predecessor, the injected red cells would disappear somewhere along *AB*; regeneration of the bleeding, if it took

place as usual, would occur as *CD*, and the actual changes in the size of the erythron would be the sum of these two processes (*AED*). In fact nothing of the kind happens. The transfused blood is not destroyed, because it is not superfluous, the haemorrhage is not regenerated because there is no need to do so. The animal has what it needs (i.e. a normal erythron), and saves itself trouble by leaving things alone' (p. 8).

2. PERSISTENCY OF ACTION

It is characteristic of animal behaviour that if the goal is not reached at once, directive action continues with or without variation of effort. The salmon encountering a waterfall on its upstream migration tries time and again to surmount it, until its leaps are successful or it falls back exhausted; there is active, persistent, long-continued effort. Here there is an element of active striving, closely similar to what we ourselves experience when trying to do a difficult job. But persistence in action need not imply conscious effort, and it may be quite stereotyped and unintelligent—that is, inadaptably to circumstances. A pair of sparrows one summer built a nest in the roof-gutter of my house, and when this was cleared away built another in the same place; several times the nest was swept away and rebuilt by the persistent birds. Nor is persistence of action limited to behaviour; it is shown also in physiological and morphogenetic activities. A good example of this is afforded by persistent egg-laying in birds, when they are prevented from accumulating a clutch of normal size in the nest. The fact is a familiar one, pointed out many years ago by John Ray (Raven, 1942), and is the original basis of continued egg production in domestic poultry.

Here are some examples. According to Bickerton (1927, p. 21), a great tit (*Parus major*) has been known to lay

25 eggs, instead of the normal 6-11, when she was left each day with only one egg in the nest; a starling (*Sturnus vulgaris*) in similar circumstances produced 40 eggs consecutively, and a moorhen (*Gallinula chloropus*) 49 eggs in 57 days. According to Herrick (1935, pp. 256-7), 'The northern flicker (*Colaptes auratus luteus*) commonly lays from five to nine eggs, but when it is systematically robbed from the time it lays its second egg, one being taken each day and one left as a nest-egg, the number it will sometimes produce is surprisingly great. The record of seventy-one eggs in seventy-three days made by a bird at Taunton, Massachusetts, beginning May 6, 1883, and reported by Charles L. Phillips, I believe has never been surpassed. . . . After years of selective breeding, certain domestic fowl have approached very close to the ideal record of an egg a day for a calendar year. In 1927 the world's duck record stood at three hundred and sixty-three eggs in three hundred and sixty-five days of continuous laying; and the record hen, a White Leghorn, laid three hundred and fifty-one eggs from November 1, 1925 to October 31, 1926. The common barnyard fowl usually lays at a definite time, and, as Glover M. Allen remarks, the presence of a nest-egg, a china one serving equally well, seems to encourage her "to keep on laying as if to attain a number whose contact stimulus would satisfy the brooding instinct"' (pp. 256-7). According to Witschi (1935) the sparrow normally lays 4-5 eggs and then becomes broody, the ovaries regressing rapidly during the incubation period through the degeneration of the larger eggs. If, however, the egg is removed daily it lays up to 50 eggs, often 12-19 on directly consecutive days.

One case is reported by Lack (1933) where provision of a clutch of two eggs apparently prevented egg-laying in the Sarus crane. A pair of these birds at Woburn had made

a nest, and the female was ready to lay when an unmated common crane laid two infertile eggs in the nest. The female Sarus, instead of laying her own eggs, started to incubate the stranger's eggs, and, the male taking turn, they sat the full period. She was not incapable of laying eggs, for later she incubated and reared her own in a new nest.

The end-state to which the physiological, morphogenetic and behavioural activities concerned in egg-formation and egg-laying naturally tend is the production of a clutch of normal size. If, through the loss of eggs, this end-state is not reached after the usual number of eggs has been laid, the bird in many recorded cases goes on laying; the organic drive to produce the normal result—so many eggs in the nest—persists, at least for some time. We know from the work of Kirkman (1937) on the black-headed gull (*Larus ridibundus*) that the bird which is ready to incubate its eggs experiences a powerful contact-need, which is normally satisfied by the presence in the nest of the normal number of eggs, or of objects which, on account of their size and roundness of contour, satisfy the contact-need of the brooding spots somewhat as well as its eggs. It seems probable then that satisfaction of contact-need is the signal that brings egg-laying to an end; when this need is not satisfied, owing to eggs being removed from the nest, egg-formation and egg-laying continue. Satisfaction of contact-need is apparently the 'normally adequate sign' that the natural terminus of egg-laying has been reached. A feeling therefore enters into the chain of events that leads to egg-laying or its cessation. This conclusion may appear absurd or paradoxical, but it is so only from the materialistic point of view. The main point I want to emphasise at the present stage of the argument is, however, simply the observed result that in many cases the combined activities concerned

in the growth of an egg, its equipping with yolk and a shell, and its expulsion from the oviduct, are repeated beyond normal measure, if the normal result is not reached by the laying of the usual number of eggs; if the normal end-state is not reached, these complex activities persist. Persistence of growth activity until a goal is reached is, of course, a common phenomenon in plants; the potato sprouting in a dark cellar sends out long white shoots, as it were in search of light; the prairie plant grows enormously long roots in its search for deep-lying water (Fig. 11, from Skrene, 1924). The wood-rot fungi extend their rhizomorphs over brick, stone or metal in their apparent search for distant woodwork. Speaking of *Merulius lacrymans*, the fungus responsible for 'dry rot', the Rolfses remark: 'The power of locomotion of this fungus is really remarkable, for it has been known to travel for yards along thin tubes containing bell-wire; it can climb up a wall from one floor of a building to

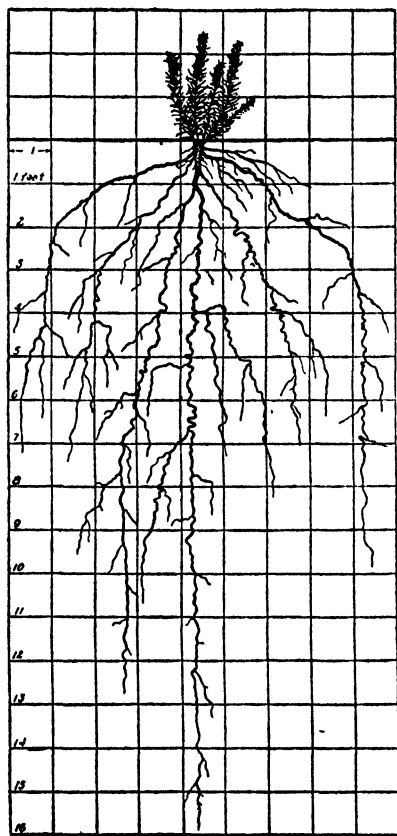


Fig. 11

the power of locomotion of this fungus is really remarkable, for it has been known to travel for yards along thin tubes containing bell-wire; it can climb up a wall from one floor of a building to

the next, and it can even penetrate brickwork through the mortar, involving in a common disintegration the walls no less than the woodwork' (1926, p. 117).

When the parasitic dodder plant (*Cuscuta*) has fixed itself on its host by closely wound coils bearing haustoria and has drawn sufficient nourishment from it, it sends out a shoot in search of another host. If this exploring shoot fails to find another host, it elongates enormously, persisting in its growth far beyond the normal span. Here is Peirce's description of such a case: 'A strong horizontal branch of *C. glomerata*, springing from the axil of a bract borne on a stem just above a region where many strong haustoria had penetrated a very nutritious branch of *Impatiens Sultani*, was allowed to grow horizontally without contact with anything, until it had reached a length of fifteen centimetres or more; then it was supported at a length far enough behind the tip to be no longer irritable. It continued to grow horizontally, and supports were applied at suitable distances. Finally, at the end of three weeks, having sent out numerous branches (which I cut...) the main branch, large, healthy, in normal condition so far as I could see, for its whole length, and still growing, had attained the surprising length of one metre' (Peirce, 1894, p. 68).

3. VARIATION OF ACTION

(a) *Persistency with varied effort*. This is most clearly shown in behaviour, both instinctive and intelligent, for here response is prompt and can be quickly changed. If the normal mode of behaviour fails to achieve its goal, it is usual for the effort to persist and to be varied. 'Persistency with varied effort', as Lloyd Morgan called it, is indeed characteristic of behaviour in general, and also of instinctive behaviour, where there is no question of intelligent adaptation of means to ends. It often happens that the

animal has several instinctive modes of action available for dealing with a particular situation, and if one fails it brings the others successively into play until the end-state or goal is attained. In his classical studies of the behaviour of the lower organisms, Jennings (1906) has described many examples of such varied action. Take, for instance, his well-known account of the responses of the protozoon *Stentor* to nocuous stimuli (pp. 170-9). If a stream of fine particles, say of Indian ink or carmine, is directed upon the disc of an actively functioning *Stentor*, no avoiding reaction is at first obtained; the *Stentor* ingests some of the particles. But soon it bends away to the aboral side, thus avoiding to some extent the irritating stream. If this reaction is not successful at first, it is repeated. 'If the repeated turning toward one side does not relieve the animal, so that the particles of carmine continue to come in a dense cloud, another reaction is tried. The ciliary movement is suddenly reversed in direction, so that the particles against the disc and in the pouch are thrown off. The water current is driven away from the disc instead of toward it. This lasts but an instant, then the current is continued in the usual way. If the particles continue to come, the reversal is repeated two or three times in rapid succession. If this fails to relieve the organism, the next reaction—contraction—usually supervenes' (p. 174). It is important to note that the order of events is not stereotyped, for sometimes the reversal of current may be tried before the turning-away response.

The third method of avoiding the nocuous stream, contraction into the tube, may last about half a minute, when the *Stentor* expands again. It does not then repeat the previous reactions, of turning away and reversing the current, but if the nocuous stimulus is still present it contracts again, repeating this response many times, during

a period of 10–15 minutes, staying in the tube a little longer each time. Finally, it ceases to expand, contracts violently and repeatedly in the tube, and breaks away its attachment to the substratum. It then leaves the tube and swims away, to form a new tube elsewhere. If, on coming out of its tube forwards, it encounters the cloud of particles, it may swim backwards and force a passage through the substance of the tube.

That is a typical example of what Jennings calls 'Trial and error' behaviour. It is directive, in that it aims at a definite end-state or goal, relief from the irritating stimulus; it shows persistency with varied effort, for if one response fails to give relief others are tried until success is achieved. It does *not* imply learning, in the sense of bettering performance through experience and repetition, but it does imply the power of varying behaviour according to the result of previous action, a power which is essentially a psychological one, a power of relating events, and acting in accordance with the situation; what one may call a practical judgment seems to be involved, as Spaier (1930) maintains with reference to instinctive behaviour in general.

There is in *Stentor*, as we have seen, no hard and fast chain of reflexes, following automatically one upon another; if one reaction succeeds in relieving the situation, the others are not carried out, but if the first fails, some other reaction is tried, and so on until, as a last resort, the drastic measure of breaking moorings and swimming away is adopted. 'The bringing into operation of any given step depends upon the ineffectiveness of the preceding ones in getting rid of the stimulating condition. The series may cease at any point, as soon as the stimulus disappears' (p. 177). It is to be noted too that the responses are not linked to a specific stimulus—*any* nocuous influence, exerted, for example, by a chemical substance or a pronounced change

in osmotic pressure, may bring about the various avoiding reactions; there is a range of danger-valences.

Persistency with varied effort is also shown when *Amoeba* attempts to ingest a *Euglena* cyst. This is light and spherical and is apt to roll away when the *Amoeba* touches it. Jennings describes and illustrates (Fig. 19) a case where an *Amoeba* followed up for 10 or 15 minutes a rolling cyst, attempting in various ways to grasp it by throwing out pseudopodia; when success was almost attained, the cyst was whisked away by the wash from a passing ciliate. 'In cultures containing many *Amoebae* and many *Euglena* cysts', writes Jennings, 'it is not at all rare to find specimens thus engaged in following a rolling ball of food. Sometimes the chase is finally successful; sometimes it is not. Many of the cysts are attached to the substratum. *Amoeba* often attempts to take such cysts as food, sending pseudopodia on each side of and above them, in the usual way, then covering them completely with its body. But it finally gives up the attempt and passes on' (p. 15). In such a case failure to reach the goal which is aimed at leads to a complete change of behaviour.

When *Planaria* is subjected to unfavourable conditions, as to high temperatures or the risk of drying up, it tries various methods of escape, turning away from the source of stimulation, at first by ordinary gliding locomotion, then by violent movements. Later it twists and turns, and finally tucks its head under its body and remains motionless. According to Mast, who has studied its reactions to increasing temperature, 'the general impression is given that as the thermal stimulus increases, the animal tries, in a sort of "hit or miss" way, every reaction which it has at command in order to get rid of the stimulation' (quoted by Jennings, p. 245).

In the behaviour of *Molanna* when repairing its case,

which we have considered above (pp. 20-22), we have already encountered a good example of persistency with varied effort. This is shown also in its righting behaviour when overturned, as described by Dembowski (1933).

The larva, it will be remembered, builds a tube of sand or other fine material, having two wings or flanges, which increase in width towards the front of the tube, and project as a canopy over its opening. There is accordingly a definite dorsal surface which is slightly convex, and a more or less concave ventral surface. When it is turned dorsal surface downwards the projecting flanges make it more difficult to right than the ordinary tubular case of other caddis worms.

Normally it succeeds in righting itself by extending its body far out to one side, gripping the bottom and pulling the case over sideways (Fig. 12). If this operation is made more difficult by placing it on a substratum of very fine loose sand, which does not afford a grip, it tries this first method repeatedly both to the right and to the left. Then it tries

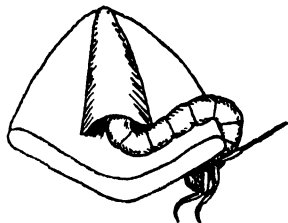


Fig. 12



Fig. 13

a second method. It reverses its position in the tube, so that its head comes out at the tail end; it widens the hinder opening of the tube by biting away some of the material and pushes its body straight out. If now some point of support is given it the body is twisted round its long axis and the case with it. Or it may turn its body right back

under the case, gripping the bottom and tilting the case right over (Fig. 13).

Another method of dealing with the situation when the substratum does not give enough grip is to bind together by threads of silk a little heap of sand to act as a holdfast and then turn by method 1. If very little sand is available, it has been observed to reverse in its tube, extend its body to its full length, and try for 10-15 minutes to pull the case to one side, as if seeking for a firmer foothold.

One extraordinary method is to bite a piece off the roof of the case, and holding it in its feet try to turn by method 1. In one instance observed by Dembowski half of the canopy and the whole of the wing on that side was gradually bitten off, and the larva managed after 6 hours' exertion to right itself by rotating the case over its damaged edge.

Finally, if all other methods fail, *Molanna* will leave its case and construct a new one elsewhere. In all its earlier attempts it never loses contact with the case.

There is no stereotyped routine of action; much variability in behaviour is shown from one individual to another. As Dembowski points out, the animal has to deal in these repair and righting experiments with situations which rarely occur in natural conditions; it cannot have learned in the course of its life how to tackle them, yet it behaves in an apparently purposive way. In *Molanna*, there is something more than the successive employment of a few stereotyped modes of behaviour, as in *Stentor*, to deal with a not unusual contingency; there is adaptability of behaviour to cope with the unusual or the unprecedented.

Stereotypy and adaptability are formally opposed; stereotyped behaviour is adjusted to the normal, adaptive or regulatory behaviour implies an active effort to deal with the unusual. But the distinction is not an absolute one, and in practice the two kinds of behaviour are interwoven with

one another; instinctive methods of dealing with the usual situation may be modified in varying degree, perhaps very little, perhaps very greatly, when the animal is confronted with an experimental situation differing from the natural one. This is shown very nicely in the experiments which Fabre carried out with the burying beetle (*Necrophorus vestigator*).

These beetles have the instinct to bury and lay their eggs in the bodies of small dead animals, or pieces of meat if they are not too large. Several may work together, removing the earth from beneath the corpse so that it sinks in, and also tugging it down. Often they have to enter the body in grass-covered soil which is permeated by the roots of the grass, and in such case they bite through the stems and roots that impede them. Fabre placed a loose mat of woven raffia below a dead mole, and found that the beetles were able to bury it without much difficulty, cutting the raffia fibres just as much as was necessary to let the mole through. This entailed little modification of the normal instinctive routine. In another experiment a dead mole was tethered to the ground by raffia strips attached to head and tail. They start to bury it, but when the earth is removed and the mole does not sink, one beetle crawls about over the corpse, comes across one of the tethers and bites through it; this end of the mole is then buried. Then finding the other end held fast they explore and cut the other string. These actions also imply little more than the ordinary routine of biting through anything that impedes the burying of the prey; there is no need to suppose that they grasp the mechanics of the situation.

A mole is tied to a vertical stick so that its head and shoulders rest on the ground; the beetles start burying this part and incidentally uproot the stick. If the stick is obliquely planted in the earth they do not uproot the

stick, but eventually climb on it and pull and shake the corpse about, and some hours later they start to chew through the feet of the mole which are tied to the stick, and happening on the raffia they bite through this, so that the mole falls to the ground. Even in this behaviour there is little more than normal procedure, for when they find in natural conditions a corpse supported on short herbage they pull at it and shake it down. If a small mouse is suspended from the stick by a wire, they succeed in cutting through the feet, but they cannot do this with a large mouse or a mole, though they work at it in vain for nearly a week before giving up—a good example of persistency in behaviour.

Greater adaptability of behaviour to an unusual situation is shown in the following experiment. Fabre placed a dead mouse on a brick which was covered by a thin layer of sand. They tried for 2 hours to bury it; then for 3 hours they pulled it about on the brick in a haphazard fashion. Later some of the males went wandering about the cage, making borings here and there, and finally they dragged the mouse off the brick to one of these spots and interred it there. There was no actual digging of the grave beforehand, for the necessary stimulus for this is the weight of the corpse on their backs as they excavate.

Many investigators, following Bethe, have called attention to the fact that if an animal is deprived of one or more of its legs, it immediately regulates its locomotory movements so as to compensate for the loss. The ordinary rhythm of progression is radically altered, but unity of action is preserved. Thus the shore crab (*Carcinus maenas*) with all legs intact moves these in a regular order when crawling forward; amputate one or more, and progression is still carried out effectively, though the order of movement of the remaining legs is changed. Progression is a function

of the neuro-muscular system as a whole, not a summation of separate limb reflexes. So, too, 'an insect which has lost a leg will at once change its style of walking to make up for the loss. This may involve a complete alteration of the normal method, limbs which were advanced alternately being now advanced simultaneously. The activities of the nervous system are directed to a definite end, the forward movement of the animal—it uses whatever means are at its disposal and is not limited to particular pathways' (Adrian, 1933, p. 468).

In these cases we have to do with an immediate physiological regulation of movements, and not, strictly speaking, with an adaptative regulation of directive behaviour, for locomotion is not by itself behaviour.

But we find a similar principle exemplified in behaviour. If the organ normally employed in a particular job is missing, shift is often made with a substitute organ, or organs, so that the normal end is attained by unusual means. The long hind-legs of the dung beetle are well adapted for impelling the ball backwards over the ground by alternating strokes, and they play the major role in this activity. But if one or both are amputated, the beetle can still push the ball along; if one only has been removed, the ball tends to move towards that side and this obliquity has to be corrected by extra efforts on the part of the stump and the middle leg of the same side; if both hind-legs are cut off, the beetle manages quite well with its middle legs and the stumps of the hind ones. With the loss of both hind-legs and both middle legs it still persists in its efforts to roll the ball along, using the end of the abdomen as well as the stumps of the legs. It even succeeds in digging the usual burrow in which to bury the ball. But if the fore-legs only are removed, the beetle is helpless; it cannot repeat the powerful thrusting movements of these limbs, by and

other organic means. These are observations made on *Gymnopleurus* by Hingston (1923, pp. 265-6).

The hunting wasp (*Sphecius speciosus*) collects cicadas for the provisioning of its larvae. Its method is to drag the cicada by main force some 20 feet up a tree and from this point of vantage to fly to its burrow, carrying the insect with its hind-legs. These have hooks which are well adapted for carrying the cicada. If the hind-legs are cut off, it carries its prey with the middle and forelegs (Howes, 1919, p. 137).

For a third example we may turn to a vertebrate. In the course of Lashley's classical experiments on the effect of brain injury on learning and retention, certain rats were subjected to spinal or cerebellar operations which interfered greatly with their powers of motor co-ordination. 'Animals which have learned the maze before the development of the motor inco-ordinations continue to traverse it, although the manner of progression may be almost completely altered. One drags himself through with his forepaws; another falls at every step, but gets through by a series of lunges; a third rolls over completely in making each turn, yet manages to avoid rolling into a cul-de-sac and makes an errorless run' (Lashley, 1929, p. 137). The goal is attained by means of movements never previously employed for the purpose. As Lashley puts it, 'if the customary sequence of movements employed in reaching the food is rendered impossible, another set, not previously used in the habit, and constituting an entirely different motor pattern, may be directly and efficiently substituted without any random activity'.

The examples here collected illustrate the fact that behaviour is essentially a striving towards an end or end-state; the effort is persistent and, usually, varied. It may be blindly persistent along one line, without material variation

of effort, especially in the case of highly specialised and stereotyped instinctive behaviour; but usually the effort is varied if success is not achieved at once.

(b) *Compensatory activity*. Where there are two or more functionally equivalent methods normally concerned in reaching a particular goal, if one is put out of action or deficient, the goal is often attained through enhanced activity of the remaining method or methods. We have seen several examples of this in Section II, and we may here recall and add to them. In the healing of wounds in the higher vertebrates three processes are involved, the active contraction of the tissues underlying the wound, whereby the exposed surface is reduced in size, the migration of epithelial cells over the wound, and their multiplication to supply the necessary number for epithelisation; in large wounds, where the need for cells is great, multiplication is more marked and goes on simultaneously with migration (see p. 17 above). Now if either contraction or epithelisation is prevented from taking place, the wound will nevertheless heal in normal time. Here is what Carrel tells us on this point. The wound scar 'is due to the collaboration of two types of tissue, the connective tissue filling the wound, and the epithelial cells, which advance over its surface from the borders. Connective tissue is responsible for the contraction of the wound, epithelial tissue for the membrane that ultimately covers it. The progressive decrease of the wounded area in the course of repair is expressed by an exponential curve. However, if one prevents either the epithelial tissue or the connective tissue from accomplishing its respective task, the curve does not change. It does not change because the deficiency of one of the factors of repair is compensated by the acceleration of the other. Obviously, the progress of the phenomenon depends on the end to be attained. If one of the regenerating

mechanisms fails, it is replaced by the other. The result alone is invariable' (1936, p. 202).

To compensate for loss of blood in severe haemorrhage, the body disposes of various converging methods, which are thus described by Carrel: 'First, all the vessels contract. The relative volume of the remaining blood automatically increases. Thus, arterial pressure is sufficiently restored for blood circulation to continue, the fluids of the tissues and the muscles pass through the wall of the capillary vessels and invade the circulatory system. The patient feels intense thirst. The blood immediately absorbs the fluids that enter the stomach and re-establishes its normal volume. The reserves of red cells escape from the organs where they were stored. Finally, the bone marrow begins manufacturing red corpuscles, which will complete the regeneration of the blood' (ibid. p. 198).

For bringing about the first step in the process, the restoration of arterial pressure and blood volume, there are two converging mechanisms—contraction of the vessels and the taking up of water from the tissues and the alimentary canal. According to Carrel 'each of these mechanisms is capable of compensating the failure of the other' (ibid. p. 203).

In both these cases, wound-healing and the replacement of lost blood, it is the attainment of the normal end-state that matters; if one contributory means towards this end fails or is deficient, the others make up for it by persisting till the goal is reached, if reached it can be.

The work of Richter and his collaborators, which we have considered in some detail in Section II, also points to the same conclusion. When the maintenance of body temperature by physiological means is upset in the rat by removal of the hypophysis and the consequent reduction in thyroid activity, the animal reacts by greatly increasing

its nest-building activity; behavioural action compensates for deficient physiological regulation. We may recall here the observations of Cannon on the cat deprived of its main physiological defences against cold; it compensates for this loss by keeping in the warm, and by increased shivering (above, p. 38). Richter's extensive experiments upon the metabolic requirements of rats show the same thing; if through operational interference the physiological means of maintaining the normal composition of the *milieu interne* are rendered ineffective, the resulting specific needs are met by appropriate behavioural action (see especially Richter, 1941). There are, for example, two methods of regulating the water balance in the body—one physiological, the other behavioural. If the first is put out of action by the removal of the posterior lobe of the hypophysis, and water is continuously lost through increased diuresis, this loss is compensated by increased ingestion of water, following upon increased thirst (above, p. 62). So, too, adrenalectomy leads to a loss of salt from the blood, but this is made up by the increased appetite for salt which results, and the consequent drinking of salt solutions (p. 73).

One further illustration. The constant need of an animal for energy to carry out the functions necessary for continued existence is normally met by the intake of food; if food is totally lacking the animal's body draws upon the stores of fat and carbohydrate it has accumulated, and in dire need upon its own living substance (p. 70).

4. ALTERNATIVE WAYS OF REACHING THE SAME GOAL

(a) It is a commonplace but striking fact that reproduction, or the reconstitution of a complete whole organism from a part of another one, is achieved in different ways, as for instance by fission, by budding, by the formation

of spores or of egg cells. The parts thus separated from the whole redifferentiate into new wholes. Particularly in plants, but in many animals as well, the same individual organism may reproduce its kind by two, or more, alternative methods. The end reached is the same, but it is reached in different ways. I do not propose to discuss in detail the relation between asexual and sexual development, which has been admirably treated by Brachet (1917), whose views I follow in my own account of the matter (1930). I shall limit attention to one particular case, that of sexual and asexual reproduction in tunicates, which has been analysed with great insight and skill by Berrill (1935 *a*), in a paper of real importance for the general theory of development.

Asexual reproduction in tunicates takes the form of budding, and it occurs in many groups (for a review see

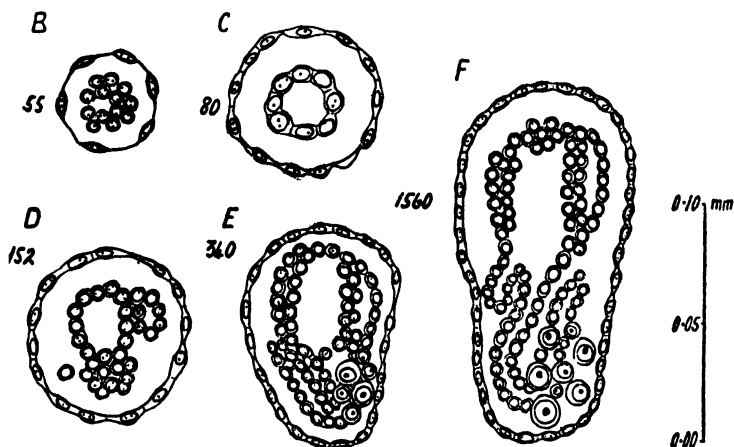


Fig. 14

Berrill, 1935 *b*). The bud is typically small and spherical on its first appearance; it consists of an outer single layer

of cells derived from the parental epidermis, surrounding a mass of cells originating from the epicardium of the parent. The outer layer forms the epidermis of the new individual, the inner cells the other organs. These cells are at first undifferentiated; they multiply by division, and there follows a rough blocking out of the main regions of the body, and then of the principal organs, such as the branchial chamber, the heart, the intestine and the gonad. Development is, as usual, from the general to the special. The essential features of the process are the multiplication of cells to form the necessary number of 'building stones' and their concomitant marshalling into place. 'It seems', writes Berrill, 'as if cells move directly to their proper relative positions as soon as cell proliferation has given rise to sufficient numbers' (p. 369). The immediate goal of cell division or cleavage is to furnish in sufficient quantity the requisite building material for the gradual formation of the organs (cf. Lillie, p. 93 above). Only when sufficient cells have been formed to enable the organs and tissues to be fully moulded into shape does cytological differentiation of the cells set in, and this differentiation appears to inhibit further cell division. The directive nature of the whole process is obvious; everything takes place with reference to the end to be reached—the reconstitution in detail of normal adult structure. In its directness and simplicity it is, as Berrill remarks, strikingly reminiscent of the cytoplasmic redifferentiation which follows division in ciliates, the only difference being that in tunicates the process is more elaborate and is complicated by their cellular state.

Exactly the same result as is achieved in budding is reached by a different path in the development of the tunicate egg; the completed organism is the same, though the mode of its reconstitution is considerably different. The egg is a single cell, usually a large one, and provided in

various degree with nutritive material or yolk. It already shows, before fertilisation, a certain cytoplasmic differentiation, predeterminative of future structure. After fertilisation it proceeds to divide, and continues to do so until the products of cleavage reach the minimal size characteristic of the species. Cleavage has nothing to do with differentiation; it merely provides suitable building stones, just as does the proliferation of cells in the bud. Thereafter follows gastrulation, and in many cases the precocious differentiation of larval structures, such as a tail, which are necessary for free-swimming life; it is mainly these temporary larval structures that are preformed or foreshadowed in the cytoplasmic differentiation of the egg. Also the number of cells produced by the cleavage of the egg is in most cases too small to allow of the complete and direct moulding of the organs of the adult, so that intermediate post-larval stages occur. In these ways, the process of development is markedly different in the egg and the bud, though the end-result is identical. Development from the egg comes close to development from a bud only where the egg is large and contains much yolk, so that it can produce through cleavage a large number of building stones, and can also dispense with special larval organs. As Berrill puts it: 'The more cells available [through cleavage] the closer is the resemblance between the development of the permanent tissues of the embryo and asexual development. The more complete the attainment of the adult organization by the developing egg, the more likely will there be a suppression of the early differentiation that results in peculiar larval organisms, since such forms no longer need be formed of necessity' (p. 418). Even in small eggs the formation of special larval structures can be omitted without affecting the final result. In the Molgulidae, for instance, some of the species have a tadpole larva, others

develop directly the adult form, and 'at the end of egg development it was hardly possible to distinguish a post-larval *Molgula* that had developed directly from one which had developed indirectly through a free-swimming tadpole stage' (p. 410). Another example of the same end being reached in diverse ways.

(b) In regeneration it often happens that a structure is reformed in a different way and from different cellular material than is the case in embryonic development; the result is the same, though the beginnings are radically different. Here are a few examples.

First, the classical case of the regeneration of the lens in *Urodeles*. In 1891 Colucci observed that if the eye was extirpated in the newt the new lens developed from the margin of the bulb. This was confirmed by G. Wolff (1895), who showed that the new lens was developed from the upper edge of the iris, a structure which in ontogeny has nothing to do with the formation of the lens. The process of lens formation from the iris (Fig. 15) is a very remarkable one. The iris consists of a double layer of epithelial cells, the inner layer of which is deeply pigmented. Cells proliferate from the top edge of the iris, forming a spheroidal mass hanging down in the position of the lens. The pigment disappears, and the cells become transparent; those in front become cubical epithelium, those behind lengthen and form lens fibres, and so a normal lens is produced in this unprecedented way. The later stages of the process are similar to those occurring in ontogeny, but the beginnings of the process are entirely different; specialised cells having no connection with the original lens dedifferentiate, multiply and redifferentiate in such a manner and in such an arrangement as to produce a typical and functional lens. It seems that what is lacking, a lens, is formed by the means nearest to hand. The organism, as Wolff says

(1894, p. 620), 'chooses the simplest way'. Thus, the same end-result is achieved as in ontogeny, but from a totally different starting point.

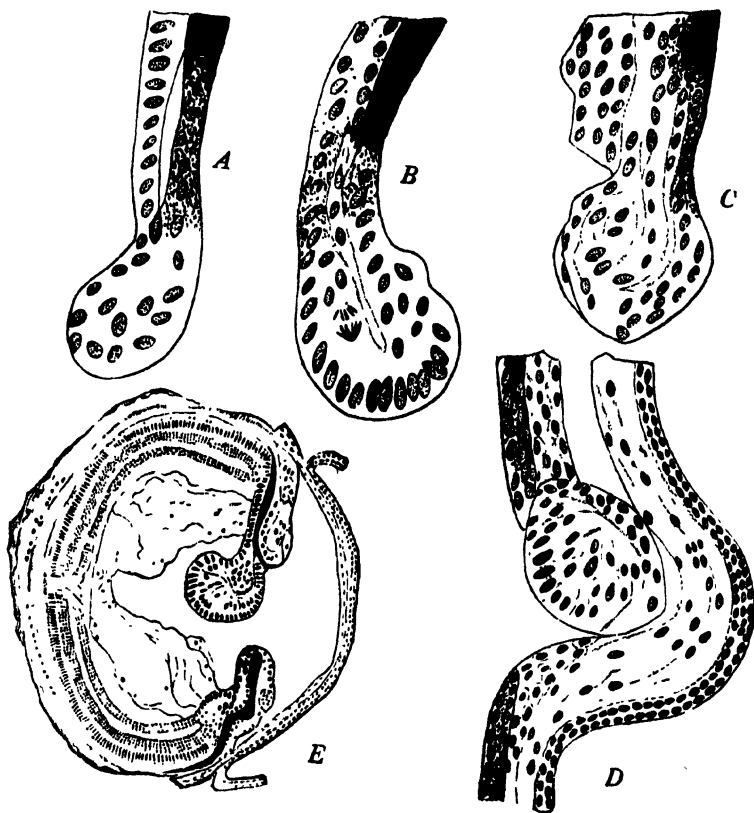


Fig. 15

Reconstitution of typical structure from unusual material is illustrated also in the following case, which I take from de Beer (1926): 'If the head ganglia of the worm *Allolob-*

phora are removed, new ganglia are regenerated. The material for these may be derived to a small extent from the remaining nervous system; but the epithelium of the dorsal wall of the pharynx undergoes dedifferentiation and gives rise to a mass of embryonic cells which is continuous with the rudiment of the new ganglia. Cells which were in the endoderm may therefore contribute to the regeneration of the nervous system in worms' (p. 89).

In the nemertine *Lineus* a small piece cut off from the head in front of the mouth and containing no endoderm remodels and redifferentiates itself so as to form a complete worm with well-developed gut, derived from mesenchyme cells; a typical result is obtained by atypical means (refs. in de Beer, p. 89).

More or less complete dedifferentiation of structure occurs in animals of comparatively simple organisation, such as hydroids and some small ascidians, for example, *Clavellina* and *Perophora*, when they are exposed to conditions unfavourable for active life. From this relatively unorganised state they can reconstitute their fully organised structure, achieving thus by different means and from different beginnings the same result as in their original development from the egg.

If in *Clavellina* the part of the body containing the branchial sac is separated from the rest, 'it may lose almost all of its organisation and become a small white sphere, consisting only of epithelia corresponding to the germ-layers, and of mesenchyme between them, and then, after a certain period of rest, a new organisation will appear. Now this new organisation is not that of a branchial apparatus but represents a very small but complete ascidian' (Driesch, 1908, p. 129). Furthermore, if the branchial sac is cut in two, in whatever direction, the pieces, if they survive, will dedifferentiate likewise, and

also reconstitute a complete though tiny *Clavellina*. The same result is achieved, on a smaller scale, as in ontogeny, but in a different way and from a different starting point.

Regeneration often takes place, not by a simple replacement of the missing parts by outgrowth from the wound, but by a remodelling and reorganisation of the remaining part—a phenomenon called by Morgan (1901) morphallaxis. A good example is the regeneration of the hydranth in *Tubularia*; when this is cut off, it is not replaced by budding out a new one, but by reconstituting a hydranth from the substance of the stem below the cut—an entirely different process from its formation in ontogeny.

The same thing is shown in a most striking way in the regeneration of planarians. I take the following facts from Morgan's admirable book. Almost any part, if not too small, will reconstitute the whole; even a marginal strip may do this successfully, though it contains none of the axial organs. Reconstitution is not a mere matter of the replacement of missing parts, except when the piece cut off is very small, but involves a certain reorganisation of the regenerating part which contributes towards the reconstitution of wholeness. If, for instance, the planarian is cut in two, either transversely or longitudinally, each half will reconstitute a typical whole, partly by new growth and differentiation at the cut edge, and partly by reshaping and drawing material from the original half, so that a complete whole is formed, generally of smaller dimensions. Thus, if the cut is made across the planarian in front of the pharynx, the posterior part will grow a new complete head, which is at first too close to the pharynx; growth then takes place in the region between the head and the pharynx until the typical distance between the two is reached. But at the same time the posterior part is altered in shape, becoming narrowed through yielding up material to the

front part, so that a complete planarian of typical shape and organisation is formed, somewhat smaller than the original. The process is shown in Fig. 16 (*A*, *C*, *C*¹), which also demonstrates the same combination of growth and reorganisation in a section cut from the middle of the planarian, and in an isolated head.

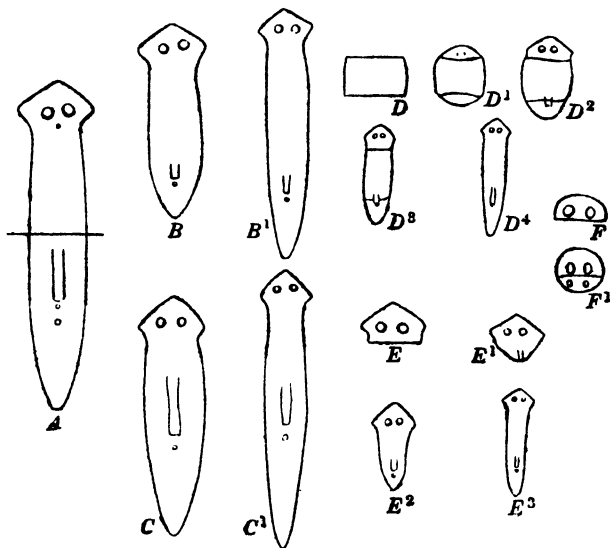


Fig. 16

The end-state to which these directive processes of growth, differentiation and reorganisation converge is the perfectly definite one, of the reconstitution of a whole planarian of typical shape and organisation, though perhaps of smaller size, and the method and course of reconstitution is entirely different from that followed in ontogeny. A somewhat similar reorganisation of the regenerating part occurs also in some polychaetes (see, for instance, Berrill, 1936).

The reconstitution of a complete organism from dissociated tissue cells is an extraordinary phenomenon which has been demonstrated to occur in certain sponges by H. V. Wilson, Galtsoff and others. In *Microciona* and *Cliona*, for example, cells isolated by squeezing a part of the sponge through fine bolting silk come together and form aggregates, which later organise themselves into little sponges. 'Under normal conditions, the essential features of sponge body, i.e. flagellated chambers, canals and spicules, are formed within five or six days. Spongin appears about the tenth day. The osculum appears by the end of the third week. . . . The rebuilding of a new sponge is due to the activities and properties of individual cells forming an aggregate. The different types of cells forming a common mass find each other and then develop flagellated chambers, skeleton, mesenchyme, and other tissues' (Galtsoff, 1925, p. 248). What greater contrast can one imagine with the normal process followed in development from the egg? A sponge is of course more an organised colony of essentially separate cells than a true metazoan organism, as Bidder (1937) has clearly shown, and more independence of action might be expected from its cells. But the phenomenon of reconstitution from dissociated tissue cells takes place also in the hydroid *Antennularia*, though here the reconstitution of the whole is not so complete (Morgan and Drew, 1913-15).

5. GOAL-DIRECTED ACTIVITY MAY BE DOMINANT OVER CONDITIONS

In the examples described above it is clear that ends or goals are more important than beginnings; the same goal can be reached from quite different starting points, and by quite different routes. It is difficult then to think of goal-directed activity as being completely determined by

its beginnings. Somehow, though we do not know how, the end or goal enters into the determination of these activities; they are, that is to say, directive.

The same conclusion imposes itself when we consider the fact that goal-directed activity is determined only in part by the conditions obtaining during its execution. When these conditions are unfavourable, the organism may yet achieve its biological ends, either completely or in a modified form. In dry or impoverished soil, for example, a plant may still achieve development and reproduction in spite of the adverse conditions, appearing in a stunted and depauperate form, which is the best that can be done in the circumstances.

A seed plant is normally dependent for its initial growth and development upon the stores of nourishment contained in the seed. If these are removed by operation or much reduced, a common result is the production of a stunted seedling. But this is not always the case. It has been shown by Raymond Pearl and his collaborators (Gould *et al.* 1934) that seedlings of the canteloup (*Cucumis melo*) from which parts of the cotyledons (containing the food reserves) have been removed show a more vigorous growth than unoperated seedlings; they are stimulated to utilise more fully and effectively the food material still remaining. Growth is not, as one might expect, proportional to the amount of food available, but considerably in excess of expectation where the amount is reduced. In fact, in the conditions of these experiments 'the larger the amount of cotyledonary tissue removed by operation the more rapid was the inherent growth rate of the seedling per unit of time' (p. 598). The seedling reacts to deficiency of normal food supply by more efficient utilisation of what remains.

Regeneration in planarians, as Morgan has shown (1901, 1902), is dependent only to a slight extent upon the food

conditions. The size of the regenerated whole naturally depends upon the amount of food and energy available; if the regenerating piece is well supplied with food it may

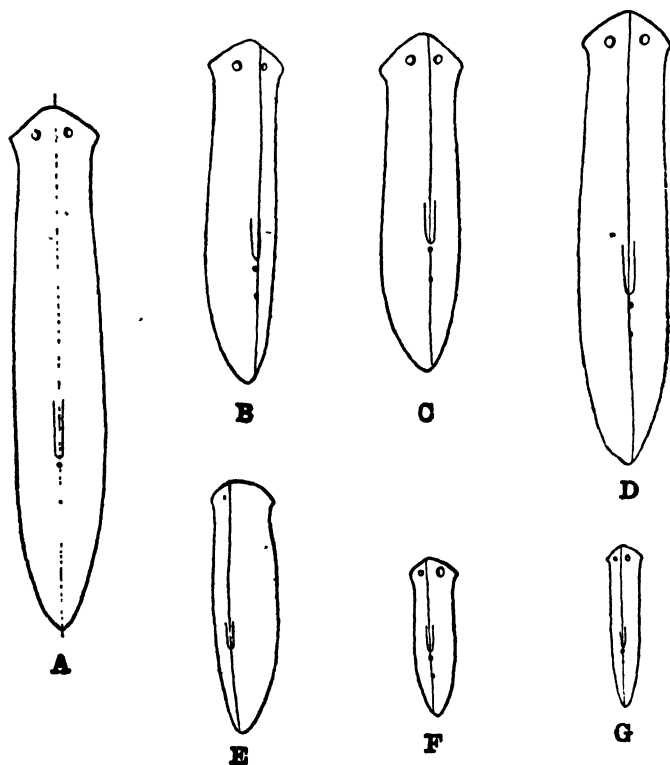


Fig. 17

reconstitute a full-sized whole (Fig. 17, *B*, *C*, *D*); if food from outside is lacking, it will reconstitute a whole of much reduced size (*E*, *F*, *G*), drawing the necessary energy and material from its own substance.

Even a planarian that has been greatly reduced in size by long-continued starvation will, if cut in two, reconstitute two new though tiny wholes. This, as Morgan points out (1901, p. 28), is a very remarkable phenomenon, and well illustrates the dominance of 'drive' over conditions, for the tissues of the regenerating halves, which are already 'slowly starving to death', are depleted still further to supply material and energy for the growth and differentiation of the new tissue formed in the reconstitution of the new wholes. We see very clearly from this example that the directive activities of regeneration are not determined, though they may be influenced, by food conditions. Utilising any source of energy which presents itself, they persist till they reach their goal. They will reach this goal if the conditions do not absolutely prevent it (as, for instance, when the regenerating piece is of too small dimensions); the conditions are not in any sense the sufficient cause of the regenerative process; they are only limiting or enabling factors—obstacles or means, which the organism if possible evades, surmounts or utilises.

In this case of the starving planarian (which is paralleled in other forms) the energies of the animal are directive towards one biological end, the restoration of normal structure, to the exclusion of others; one might put it that the drive to completion is dominant over the need for food of the starving cells; material which is urgently required for nourishment is diverted and utilised for the remodelling of structure.

We encounter much the same phenomenon, of dominance and subordination, in the relation of reproductive to maintenance activities. The salmon starves while its accumulated stores of fat go to the building up of its gonads; the lactating mammal may suffer softening of its bones through the withdrawal of calcium required for the milk; the

partridge may sacrifice her life in the protection of her young (Ogilvie, 1920, p. 50). In all such cases, which could be extended indefinitely, the reproductive drive is dominant over the needs and drives of self-maintenance or self-preservation.

Looking back over the characteristics of goal-directed activity which we have considered in this section, we see that such activity does not fall into line with that shown in the inorganic world, but is clearly separate and distinct. Coming to a definite end or terminus is not *per se* distinctive of directive activity, for inorganic processes also move towards a natural terminus; the moving stone rolls down the hill till it reaches the bottom, or is stopped by some obstacle; the unstable system moves towards a stable equilibrium; the same stable equilibrium may even be reached from different starting points. What is distinctive is the active persistence of directive activity towards its goal, the use of alternative means towards the same end, the achievement of results in the face of difficulties. Goal-directed activity is no mere resultant of material conditions, as is the case with inorganic systems; there is in it an element of effort or striving, which sometimes, as in our own purposive behaviour, becomes conscious of itself and its aims, but is more often unconscious and blind. It is not dominated by conditions, but strives to surmount or utilise them in its movement towards its goal. One drive may dominate another.

This element of drive, effort or striving (which we experience in its highly developed form as conation) is one factor in all vital activity, behavioural, physiological and morphogenetic, which essentially distinguishes it from inorganic action. That at least is the view to which I have come; I shall develop its implications later. That living things have a certain autonomy of action which distin-

guishes them from the non-living is a view expressed with clarity and force by Grainger (1940) in a discussion of the nature of viruses. 'Autonomous movement,' he writes, 'or motion controlled by the organism itself, gives the first real clue to the quality of life. Living things are not completely at the mercy of their environment, whereas non-living matter has a totalitarian subjection to external surroundings. Thus a non-living mass of protein always rolls down a slope with unquestioning obedience to the law of gravity; living protein in certain forms *can* move up the slope, following its internal direction. . . . Motile bacteria can move against a slight stream of liquid' (p. 539). This autonomy of movement in opposition to physical forces is shown, according to Grainger, by certain viruses which disperse themselves actively in their plant host; these may be ranked accordingly as living organisms.

It is interesting to note that the characteristics of goal-directed activity which we have distinguished are very similar to those which William McDougall has singled out as characteristic of behaviour. They are as follows. First, 'a *certain spontaneity of movement*. In behaving, an animal is not simply pushed or pulled by forces external to itself; but if it actively resists the push or pull, it is behaving'. A second mark of behaviour is 'the *persistence of activity independently of the continuance of the impression which may have initiated it*'. 'Variation of direction of persistent movements is a third mark of behaviour.' The fourth is cessation of activity when the goal is reached—'the *coming to an end of the animal's movements as soon as they have brought about a particular change in its situation*' (1923, pp. 44-5). A fifth characteristic is the anticipatory or proleptic nature of much behaviour. These are all characteristics of goal-directed activity in general.

Behaviour, as we have seen, is just one of the means or methods of action through which the living organism

achieves its biological ends; physiological and morphogenetic activities are also means or methods, functionally equivalent to behavioural action. It is not astonishing then that they should have the same characteristics as behavioural action, for all three share the fundamental character of directiveness.

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EXAMPLES OF CONSTRUCTIVE AND
CREATIVE ACTIVITY

1. At the beginning of this book (p. 8) I singled out as characteristic of living organisms the directiveness and creativeness of their activities. Directiveness we have considered in the last few sections; we may turn now to study creativeness, as shown especially in the development of the living being. I use the word creativeness deliberately, for no other appears adequate to describe the amazing power which living organisms possess of building up from simple beginnings, through their own activity, elaborate functional organisations of extreme complexity and adaptability.

The familiar becomes all too easily the commonplace, and for that reason alone we are apt to forget just how remarkable a process development is. The separation of biological studies into closed compartments also tends to obscure from us the wonder of development. Embryology deals mainly with the earlier stages of the process, with the first roughing out of the organs and tissues, and does not carry us as far as the fully formed adult; also it is chiefly interested in structure rather than function. There is little connection between it and the physiological study of the adult and functioning organism. Physiology has given us much insight, especially in the higher mammals, into the extraordinarily complex and self-regulating organisation, both structural and chemical, which is involved in the everyday functioning of the fully formed animal body and in its response to varying needs. But when we read the

books of Cannon or Haldane or Sherrington, for example, which unveil part of this amazing complexity of interrelated function, do we pause to consider that all this is built up afresh, in the course of individual development, from a single microscopical cell, with the help of the most elaborate structural and physiological provisions in the body of the mother for the protection and nourishing of the developing embryo?

The marvel of development, as manifested in the building up of an extreme complexity of structural organisation and the emergence of new functional capabilities as differentiation proceeds, is well characterised by Conklin (1916) in the following passage. Referring to the fertilised egg cell of starfish, frog or man, he writes: 'Under proper environmental conditions this fertilised egg cell develops, step by step, without the addition of anything from the outside except food, water, oxygen, and such other raw materials as are necessary to the life of any adult animal, into the immensely complex body of a star-fish, a frog, or a man. At the same time, from the relatively simple reactions and activities of the fertilised egg there develop, step by step, without the addition of anything from without except raw materials and environmental stimuli, the multifarious activities, reactions, instincts, habits and intelligence of the mature animal. Is not this miracle of development more wonderful than any possible miracle of creation? And yet as one watches this marvellous process by which the fertilised egg grows into the embryo, and this into the adult, each step appears relatively simple, each perceptible change is minute; but the changes are innumerable and unceasing and in the end they accomplish this miracle of transforming the fertilised egg cell into the fish, or frog, or man—a thing which would be incredible were it not for the fact that it has been seen by hundreds of observers and

can be verified at any time by those who will take the trouble to study the process for themselves' (pp. 22-3).

The wonder of development is celebrated in a most vivid, even lyrical fashion, by Sir Charles Sherrington, and his testimony is the more remarkable because he is, in the matter of physiological method, an avowed mechanist (see p. 181 below). In the human child at birth, he tells us, there are some 26 million million cells: 'They have arranged themselves into a complex, which is a human child. Each cell in all that more than million-fold population has taken up its right position. Each has assumed its required form and size in the right place. The whole is not merely specific but is a particular individual within the limits of the specific.

'In that individual, that "persona", each cell has taken on the shape which will suit its particular business in the cell-community of which it is a member, whether its skill is to lie in mechanical pulling, chemical manufacture, gas-transport, radiation-absorption, or what not. More still, it has done so as though it "knew" the minute local conditions of the particular spot in which its lot is cast. We remember it is blind; senses it has none. It knows not "up" from "down"; it works in the dark. Yet the nerve cell, for instance, "finds" even to the finger tips the nerve cell with which it should touch fingers. It is as if an immanent principle inspired each cell with knowledge for the carrying out of a design. And this picture which the microscope supplies to us, supplies us after all, because it is but a picture, with only the static form. That is but the outward and visible sign of a dynamic activity, which is a harmony in time as well as space' (1940, p. 106).

Of the differentiating cells in development he writes with poetic fervour yet with accuracy: 'They, as the case may require, pour out cement which binds, or fluid in

which they shall move free; or they hold hands for surer and more sensitive contact. Some will have changed their stuff and become rigid bone or, harder still, the enamel of a tooth; some become fluid as water so as to flow along tubes too fine for the eye to see. Some become clear as glass, some opaque as stone, some colourless, some red, some black, Some become factories of a furious chemistry, some become as inert as death. Some become engines of mechanical pull, some scaffoldings of static support. Each one of all the millions upon millions finally specialises into something helpful to the whole. . . . It is as if the life of each one of all those millions has understood its special part. Thus arises the new integral individual to be' (p. 107).

Development appears to proceed according to a fixed and invariable plan, and there is something mysterious and almost uncanny in the way in which the specific type is reproduced. This aspect of development has been emphasised very aptly by Duhamel in one of his novels (1938), and the passage is worth citing: 'Voilà les cellules qui se multiplient à partir de l'œuf. Et, toujours, elles vont pousser dans le même sens, se replier au même endroit. Toujours, en un point déterminé, les cellules, à un moment déterminé, vont engendrer quelque chose comme un poil, ou comme un ongle, ou comme une glande. Pourquoi? Et à telle place, dans le pelage ou le plumage, une tache du même rouge ou du même gris, toujours la même. Pourquoi? Je le demande. Il est impossible d'expliquer ces choses, et ces choses sont l'essentiel, et ces choses sont les seules qu'on voudrait vraiment comprendre' (p. 220).

2. In a previous section (pp. 93-7) I have given some illustrations of the directive and proleptic nature of the activities concerned in development. Here I shall limit attention to one aspect only of the developmental process, that, namely, which involves the constructive activities of

cells working in concert to produce, by secretion and absorption, highly complex and biologically purposive structures. Such constructive or building activities play a great part in the development of most living creatures, especially in the formation of their supporting and protective tissues, and, in plants, of their conducting tissues also. They are perhaps easier to understand than the development of tissues and organs through the multiplication and differentiation of the cells themselves, having a somewhat closer analogy with human constructive activity. As master builders in this mode, using material which they themselves secrete, the cells of plants take pride of place. For the most part they form definite cell walls, and most of the intimate architecture of the plant arises through modification in the shape of its cells and elaboration of the structure of their walls.

As an example let us consider in brief outline the structure and development of the stem of a dicotyledonous plant in its simplest form, uncomplicated by the formation of secondary wood.

The familiar cross-section of a sunflower stem shows at its periphery an epidermal layer of cells with strongly thickened outer walls. This is continuous, except where interrupted by stomata or lenticels, forming a resistant sheath round the stem, and its function is protective and supporting. Inside the epidermis there is a layer of elongated collenchymatous cells with thickened longitudinal walls, whose function is support. Thin-walled cortical cells succeed these, surrounding the starch-sheath which encloses the central cylinder or stele. Immediately inside the starch-sheath is a zone of tissue composed of bundles of fibres and of parenchyma which is known as the pericycle. In the stele the most conspicuous structures are the radially disposed vascular bundles surrounding the

central pith. These are composed of three types of tissue, the phloem on the outside, the xylem on the inside, and the cambium in between, together with intercalated parenchyma cells. The structure of the cells making up the vascular bundle is best seen in radial longitudinal section, as shown in Fig. 18. The phloem is made up of sieve-tubes

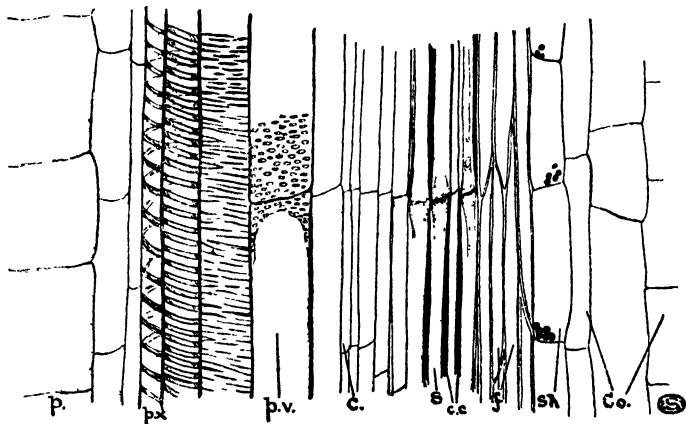


Fig. 18

with their companion cells. The sieve-tubes (*s*) are elongated cells, arranged end to end, separated by terminal sieve-plates, through the pores in which the protoplasmic lining of each cell is continuous with that of the cell above and the cell below. Their function is to mediate the long-distance transport of albuminous food material from the leaves downwards towards the root. They early lose their nucleus; the companion cells (*c.c.*) are sister cells of the sieve-tubes, having densely granular protoplasm and retaining their nucleus.

The principal cells of the xylem are the vessels whose function is the conduction of water from the roots upwards.

They are vertical files of cells whose transverse walls have been absorbed, so that they form continuous tubes of some length. Their walls are strengthened by internal spiral or reticulate thickenings which serve to hold them open. In their mature state they have no protoplasmic content; they are dead, but the mechanically purposive structure they have formed persists to play its part in water conduction.

The third element of the vascular bundle, the cambium, is composed of flattened thin-walled cells (*c*), which retain the power of forming additional vascular tissues, both phloem and xylem.

The elaborate structure of the stem as a whole is nicely adapted to the functions it has to perform. The rigidity and upright position of the stem are ensured in part by the turgor of the parenchyma and pith, these internal tissues being held in a state of compression by the resistant epidermal layers. This turgor effect is reinforced by the structure and disposition of the subepidermal collenchyma and xylem, which function as mechanical supporting tissue, and as the stem increases in size additional mechanical tissue is formed by the development of fibres in the pericycle. Fibres are very long narrow cells with thickened walls; in their mature condition the protoplast has disappeared, so that, like the fully formed vessels of the xylem, they function in virtue of their dead structure. The supporting tissues are found towards the periphery of the stem, where they are most effective in resisting lateral pressure. The stem also serves the purpose of conducting water from the roots to the leaves, and of the products of assimilation from the leaves downwards, and we have seen how the vessels of the xylem and the sieve-tubes of the phloem are specialised and adapted for these functions.

Now this highly organised and biologically purposive architecture of the stem, subserving the vital needs of the

plant, is developed solely through the metamorphosis, at the right time and in the right place, of the undifferentiated cells formed from the growing-point of the stem, and especially through their changes in form and the modifications of their secreted cell walls. Consider, for instance, the development of the tissues of the vascular bundles. 'These first appear in the axis a short distance behind the tip as so-called *procambial strands*, composed of very narrow, elongated, thin-walled cells with tapering ends, dense protoplasmic contents, and prominent nuclei. They develop by repeated longitudinal division of certain cells of the meristem, in which transverse division almost ceases at an early stage, the narrow segments thus formed subsequently elongating. In the stem each procambial strand gives rise to a vascular bundle, whilst in the root there is usually a single strand from which the whole vascular cylinder is differentiated. The innermost elements, in each of the procambial strands of the stem, become the spirally thickened protoxylem-vessels, whilst simultaneously the outermost elements develop into the first-formed phloem (*protophloem*). As the strands are traced farther and farther from the apex (i.e. from younger to older stages) the differentiation of xylem and phloem proceeds towards the middle of each. Ultimately all that remains is a narrow strip of thin-walled cells between xylem and phloem, which in Dicotyledons gives rise to the cambium' (Fritsch and Salisbury, 1938, pp. 146-7).

There are two remarkable things combined in this development of the vascular bundles—the differentiation of the cells themselves, and the establishment and maintenance of their proper spatial and functional relations to one another. The differentiating bundles appear from the beginning in their proper place; there is not a haphazard differentiation here of a sieve-tube, there of a vessel, but an

orderly formation of a typical number of vascular bundles, properly situated with respect to one another, and in each developing bundle the elements of the phloem, the xylem and the cambium appear in their normal spatial relationship. The differentiation of each kind of cell takes place by the specific differential growth of its cell wall, as a result of the *directive* secretory activity of its protoplast; but this differentiation of the single cell is not independent of the differentiation of neighbouring cells—as is clearly shown, for example, in the formation of sieve-tubes and vessels. Each sieve-tube differentiates in relation to the next in series, establishing protoplasmic continuity with it through the strongly developed intercellular connections which pass through the wide pores in the sieve-plates; the elements of the xylem, developing in vertical file, acquire a continuous lumen through the dissolution of the transverse cell walls that originally separated them; each develops in relation to the next, and in such a way that a continuous vessel is formed, apt for its function.

It is this orderliness of the process, the occurrence of growth and differentiation in each cell at the appropriate time and place, in relation to its neighbours and to its position and future function in the whole stem; that is so striking.* This is a characteristic feature of organic creative activity, as shown in development generally. When we think of the development of the plant stem, or of the formation of organs and organ systems in the animal embryo, as being due to the activities of the cells concerned in building them up, we must recognise that the essential thing is the orderliness of these activities with reference to

* Cf. Sherrington, 1940: 'Each of the cells from the beginning besides shaping itself takes up for itself a right station in the total assembly according to the stage which the assembly has by that time attained. Thus each cell helps to shape, and to construct as by design, the total assembly and the assembly's ordering of the moment' (p. 105).

one another and to the end-state to be reached; without such orderliness development could not proceed successfully nor reach its goal.

It is this feature, of the harmony or proper timing and spacing of activities in relation to the end-state to be reached, that makes any purely physico-chemical study of development so inadequate. No doubt many physico-chemical laws hold good in the living body, and it may well be that many of the single events in development take place in strict accordance with these laws. The dissolution of the transverse walls in the formation of the vessels in the plant stem is presumably brought about by physico-chemical means, and a complete physico-chemical account of it may well be feasible. But such an explanation would not touch the real heart of the problem, which is to discover how this action occurs at the proper time and place, and so plays its essential role in the orderly differentiation of the whole stem. It is not the mechanism of the action that is important, but the integratedness of the action in the developmental process as a whole.

The problem of the orderliness of development cannot be completely solved, since some degree of orderliness must be assumed to exist even in the egg cell, which is itself a living and organised unity. But the conditions in which a particular activity arises in the course of development, and the stimulus which elicits it are certainly open to investigation. It is this line of approach that functional biology should adopt, leaving to biophysics and biochemistry the investigation of the details of action. It will be remembered that we reached a similar rule of method after considering the activities concerned in the restoration of norms and the satisfaction of needs (p. 77).

The pursuit of a completely mechanistic account of the organic activities concerned in development is in fact a

hopeless undertaking, for no mechanistic explanation can account for the orderliness and directiveness of organic activities, their harmony and co-operation towards biological ends, which is so strikingly shown in the development of the organism. This harmony and co-operation can, however, be investigated from the point of view of functional biology, on condition that we think in terms of living units and their activities, and not in terms of mechanisms. Actually, considerable progress has been made towards a biological account of the orderliness of development by the discovery of evocators and growth hormones, which are the normally adequate stimuli for certain morphogenetic activities.

3. As a second example of the constructive activities of cells working in concert with one another we may take the formation of the spicules in calcareous sponges. As is well known, the supporting elements which are necessary to give some degree of consistence and rigidity to the sponge organism are, in the various groups, either calcareous or siliceous spicules, or a web of spongin fibres often with intermingled siliceous spicules and extraneous substances; few sponges lack this stiffening altogether. Sometimes, as in the simpler calcareous sponges, the spicules remain quite separate from one another, though arranged in an orderly manner in relation to the need for support or protection. In other forms, and especially in the Hexactinellida, with their six-rayed siliceous spicules, a very elaborate and rigid skeleton may be formed by the interlocking and fusion of spicules of diverse shapes and sizes, according to a predetermined pattern. The classical example of this is the beautiful skeleton of *Euplectella*, with its intricate lace-work of longitudinal, transverse and diagonal fibres, well adapted to support it in the abyssal depths in which it lives (see Minchin, 1900, p. 120, and

Fig. 15). Many of this group, living on a mud bottom, have specially developed tufts of long spicules, in *Hyalonema* 2 feet or more in length, which serve to anchor them in the mud (Minchin, *ibid.* Fig. 19).

These elaborate skeletal structures are formed by the secretory activities of cells, which produce spicules of the appropriate size and shape at the proper times and places. All sponge spicules, whether siliceous or calcareous, are in fact formed by the secretory activity of one or more cells. In the Calcarea, which we shall especially consider, 'the whole growth of the spicule or spicular element is entirely due to the activity of the original scleroblast and its descendants. The mother cell divides into a greater or lesser number of formative cells which spread over the growing spicule and build it up to the required size' (Minchin, 1900, p. 41). The process has been described with great clarity in the Ascons by Minchin (1898, 1908), whose account we may follow here.

In *Clathrina*, an Ascon sponge of simple structure, the supporting elements consist of a set of triradiate spicules embedded in the external or dermal layer, and of quadri-radiate spicules lying in the internal or gastral layer, their fourth ray, which arises from the centre of their triradiate basal system, projecting into the gastral cavity, between the collar cells. All these spicules are separate from one another, but they are orientated in such a way that one ray always points downwards from the osculum.

The quadri-radiate spicule is essentially a triradiate spicule with a fourth element added, and the triradiate system develops in the same way in both kinds of spicule. It is formed by cells that migrate inwards from the dermal flat epithelium. They approach one another to form trios of cells closely apposed in a trefoil pattern. Each of the cells in the trefoil then divides in such a way that there are

formed two superimposed trefoils, one external and one internal with reference to the dermal surface. These cells may be called the outer and inner formative cells respectively; they form a sextet. 'The sextet is now ready to secrete the spicule, and the first preparation for this event appears to consist in a fusion of the formative cells at the centre of the sextet; if not actually fused, the cells are at least in such close contact that their limits are indistinguishable towards the interior. The young triradial

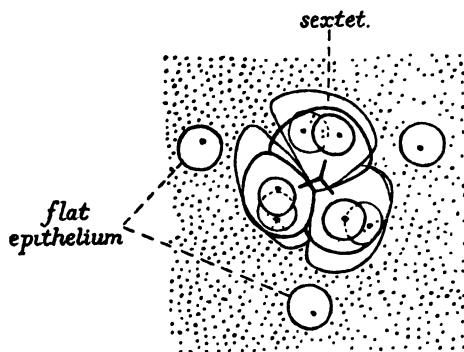


Fig. 19

spicule appears in the central portion of the sextet, and is so placed that each of its rays corresponds to one of the three pairs of formative cells' (1898, p. 506). The state of affairs at this stage is shown diagrammatically in Fig. 19.

At first the three rays are separate from one another, but they soon fuse at the centre to form the triradial system. They are very small at first and completely embedded in the formative cells, but they soon grow to a length far exceeding the diameter of these cells. During this process the inner formative cell of each accompanies the apex of the growing ray, while the outer formative cell

stays at the base of the ray, as shown in Fig. 20. The spicule is covered everywhere by a thin layer of protoplasm, and is in its origin an intracellular formation. The apical cell is responsible for the lengthening of the spicule, but later it disappears; the basal cell builds up the base of the spicule to its full thickness and 'then migrates slowly towards the

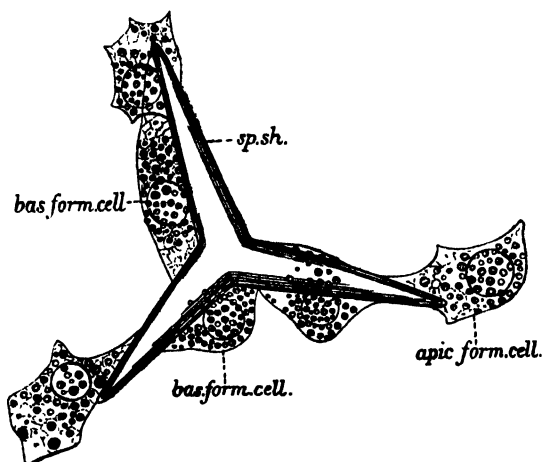


Fig. 20

tip, building up the spicule as it goes, till finally in the fully formed spicule we find the definitive spicule cell persisting at the extreme tip of the spicule' (1898, p. 513).

The triradiate part of the quadriradiate spicule is formed in the same way, but there is superadded to it at an early stage a fourth or gastral ray, which is secreted by a mother cell of different origin from those forming the triradiate part, being derived from a porocyte. This cell attaches itself to the centre of the developing triradiate system, and

secretes its ray in the proper place and orientation (Fig. 21).

This is a very fine example of the co-operative activity of cells towards the production of a structure of characteristic shape and form. The porocytes come from the dermal epithelium, the cells of which in the allied genus *Leucosolenia* have the power of secreting monaxon spicules; there is therefore nothing very remarkable in the fact that the porocytes of *Clathrina* can produce monaxons. But we

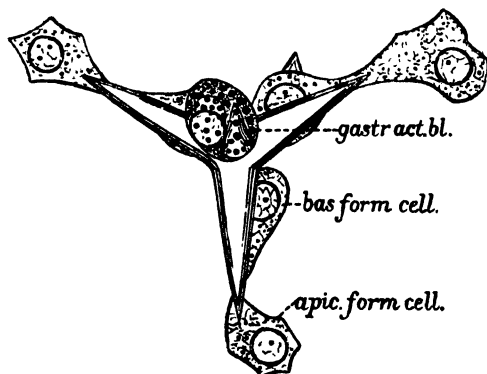


Fig. 21

are quite at a loss to explain 'why the presence of a young triradiate system in the vicinity should stimulate the porocyte to resume its long-forgotten functions, nor, above all, why it should not only secrete a monaxon spicule, but should go so far as to stick it on to the triradiate system. The formation of the gastric ray is, indeed, a most crucial test of the theories of spicular origin, and all simply mechanical theories are at once, as it were, impaled upon its relentless point' (1898, p. 562).

The monaxon spicules in *Leucosolenia* to which reference has been made are long slightly curved structures, which

project from the surface of the sponge, and end in a spear head or bayonet point; their function is protective; they are probably shed and renewed as required. Their mode of formation closely parallels the development of a single ray of the triradial spicule. The first sign of the formation of a monaxon spicule is the division of the nucleus of a dermal epithelium cell, followed by an incomplete division of the cell body. Inside this binucleate mother cell the spicule is secreted in the form of a thin rod. The mother cell then completes its division into two cells, of which one moves inwards to form, as it goes, the shaft of the spicule, while the other remains near the point and forms the spear head. These stages are shown in Fig. 22. So far the young spicule is inside the body wall, but it soon pushes forward through it and protrudes freely into the water. As the spicule continues to lengthen, the distal cell, having finished its work of making the spear head, moves back and helps to build up the shaft. When the spicule is fully formed both cells leave it.

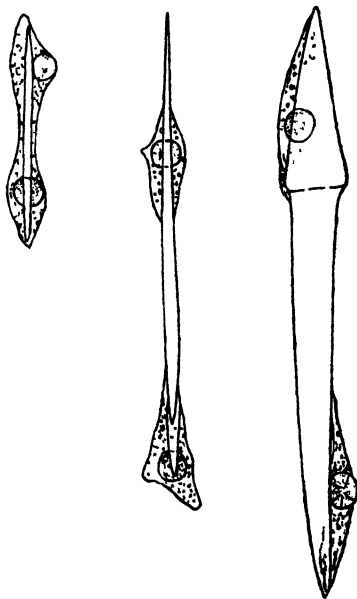


Fig. 22

The spicules of calcareous sponges, being formed of calcite, which is a crystalline substance, owe their shape in part to their crystalline nature. But only in part. They

are actively secreted in a particular shape by formative cells, and this shape has normally a functional significance. 'The fitness of the triradiate spicules for supporting the body-wall is obvious to anyone acquainted with the structure and life conditions of the sponge', writes Minchin (1908, p. 335), and the monaxon spicules are clearly protective in function. Their shape is certainly not mainly due to the crystalline properties of their substance. 'To begin with, they always have unlike poles, which is a point of difference from any crystalline body, but which can be correlated with their situation in the body-wall, one end being embedded in the tissues, the other projecting free into the water. . . . The frequent presence of a distinct barb at the free distal end is a character which may be regarded as increasing the efficiency of the spicule as a protective weapon, and', Minchin adds, 'I would invite those who find such an explanation too teleological for their taste to put forward an alternative theory, and to explain the presence of the barb on mechanico-physical grounds' (1908, p. 336). The particular shapes of sponge spicules are in the main of functional significance, and are due to the directive secretory activities of their mother cells, which form them in the right spot at the right time.

Here is a rather striking example of the orientation of spicule formation in relation to future requirements. In *Leucosolenia*, as in *Clathrina*, the triradiate spicules in the oscular tube are all arranged in such a manner that one ray points away from the osculum; this arrangement also holds good in the blind diverticula which arise from the main tube; in all these cases the unpaired ray points against the current which is generated by the activity of the collar cells, and flows out through the osculum. In the blind diverticula, then, the unpaired ray is directed towards the blind end. But when the diverticula grow to

a certain length, oscula are formed at their extremities, perforating the blind ends. Before the new oscula are formed, however, a remarkable change takes place in the arrangement of the spicules. 'In diverticula which *still end blindly at the apex* it is seen that a short way from the apex the spicules become confused in arrangement and that from chaos an orderly arrangement again emerges, in which, however, the disposition of the triradiates is exactly the reverse of what previously obtained; the unpaired ray points away from the blind apex of the diverticulum instead of towards it' (Minchin, 1908, p. 332). Thus when the osculum is formed at the end of the diverticulum, the newly formed triradiate spicules have already taken up the arrangement which is typical for these spicules in a functioning oscular tube. Such proleptic or anticipatory activity is of course a well-known and widespread phenomenon in development, to which we have already called attention (p. 93).

4. Leaving the sponges with their simple 'colonial' organisation, built up of separate cells (see Bidder, 1937), let us turn for our last example of the constructive activity of cells to the highly organised vertebrate type, and consider the main features in the development of 'replacing' bones, those, namely, that are preformed in a small cartilaginous model of the bones-to-be. The development of the long bones, with their highly elaborate functional structure, is perhaps the most striking example known of the architectonic activity of co-operating cells, but the story is much too long and complicated to be told here in any great detail. It will be sufficient for our purpose to describe in bare outline one comparatively simple case, the early development of the limb bones in the chick embryo, as worked out by Miss H. B. Fell (1925).

A limb-bud in the early embryo is composed of Im-

differentiated mesenchyme cells covered by epithelium, and the first sign of the formation of the cartilaginous elements of the limb is a condensation of the mesenchyme cells at the site of the future cartilage. Chondrogenesis begins at the centre of the shaft-to-be, where the cells become elongated transversely to the long axis, and secrete the cartilaginous matrix. 'The transverse elongation of cells soon spreads to the ends of the diaphysial portion of the shaft, and simultaneously a slightly different arrangement of the cells is seen. Their long axes no longer lie along straight transverse lines, but on ellipses convex to the future epiphyses; at the centre of the diaphysis is a narrow lozenge-shaped area, occupied by more or less polyhedral cells, where the two series of ellipses meet. This elliptical configuration is most marked toward the end of the diaphysis where the curvature of the lines is greatest' (p. 421). In this way the size of each developing skeletal element is mapped out, and the line of demarcation from the neighbouring element indicated. At this region of demarcation, where two opposed systems of arcs approach each other, a joint will later be formed. At first very young cartilage matrix extends across the line of the future joint, but it ceases to develop and finally disappears (Murray, 1936, p. 21). Thus in quite an early stage of development the future architecture of the skeleton of the limb is foreshadowed in general plan. It is noteworthy that the skeletal elements that are formed are not of equal size, nor are the joints equidistant, but each is blocked out in proportion to the size that it will attain in later development. The formation of the cartilaginous model of the future skeleton of the limb proceeds therefore according to an orderly plan; the cartilage is laid down at the right place and at the right time to bring about the formation of elements of the right size and shape, with reference to

what they will ultimately become. It is a remarkable fact, demonstrated experimentally, that the separate skeletal rudiments develop to a large extent independently of one another, the developing skeleton of the limb being a mosaic of self-differentiating parts, not greatly influenced by their relations one to another. Having grafted the basal fragment of a posterior limb-bud from a 4-day chick embryo on the chorio-allantois of an older embryo, Murray and Huxley found that the graft developed a nearly typical femur, without any other skeletal parts except a small ectopic piece of cartilage. This is shown in Fig. 23. In the complete absence of a pelvis there was developed a practically normal head, and the femur showed its normal curvature. Chondrification had proceeded according to plan, and produced a femur of approximately the right shape. Later, Murray described 'another femur having a well-developed head, in the absence of the pelvis, a femur having condyles in the absence of tibia and fibula, and a humerus having condyles in the absence of radius and ulna' (1936, p. 14). All this typical formation is brought about by the orderly activity of the chondroblasts concerned.

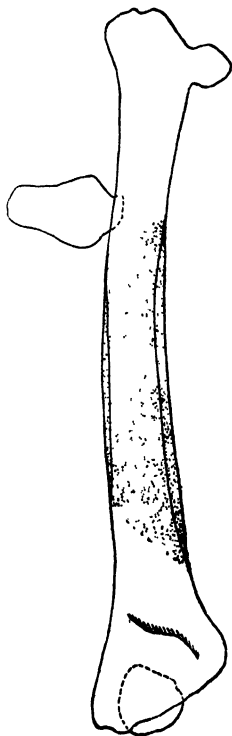


Fig. 23

Having given our attention to the orderly directiveness of the cellular activities concerned in the formation of the cartilaginous elements of the limb skeleton, we may now go on to consider in outline the formation of the bones.

At an early stage there is developed round the central part of the cartilaginous shaft a layer of oblong cells, the perichondrium, which soon differentiates into two layers, an outer layer of fusiform cells which become fibroblasts, and an inner of rounded or oval cells which become osteoblasts. Developing blood vessels appear in the outer layer of the perichondrium. 'The first signs of ossification appear in the osteoblastic layer investing the middle region of the cartilage, where the bone is formed as delicate, undulating laminae composed of fine interwoven fibres cemented together by an amorphous material which becomes more conspicuous as development advances. These laminae are intercellular structures running parallel with the long axis of the cartilage, and are first developed near the line of junction of the cartilage and perichondrium' (Fell, 1925, p. 428). Ossification spreads gradually towards the ends of the shaft, while centrally the lamellae fuse to form a thin compact cylinder of bone lying between the perichondrium and the cartilage. The osteoblasts enclosed during this process become bone corpuscles. The central cylinder thickens, and there are formed on its outside bony trabeculae, adherent to it, in the osteoblastic layer which is now rich in blood vessels. These trabeculae tend to radiate from the original centre of ossification; they grow in length and a second series of bony lamellae are formed outside them, concentric with the central cylinder. 'As ossification continues, the bony trabeculae become thicker and their interconnections increase in size and number until at length the blood vessels become completely enclosed in continuous radiating tubes—the haversian canals' (p. 432). Before this happens, the original cartilage round which ossification takes place is eroded and the marrow cavity of the bone is formed. Blood vessels from outside burst through the central cylinder of bone at various points

and penetrate into the cartilage, which appears to dissolve in front of them; large spaces are thus eaten out which later coalesce to form a single large cavity lying in the central part of the shaft, in which typical marrow tissue develops. There is in the chick no endochondral ossification such as occurs in mammals, except at the ends of the diaphysis and in the epiphyses, where cartilage is replaced by cancellated bone formed in the walls of infiltrating outgrowths from the marrow tissue. The process of bone formation is therefore somewhat simpler in the bird than in the mammal, but in both it results in the production of a highly organised structure, preadapted to the various functions it has to perform. The orderliness and directiveness of the complex activities concerned is most striking.

We have now considered some examples of the constructive activities of cells and cell groups working together to build up biologically purposive structures. We may note in passing that constructive ability is shown also by many animals that make nests or burrows, spin cocoons or weave snares, build protective tubes around themselves of many kinds. Usually they work singly, drawing the material of their art from their own body or from outside or from both sources. But, in insect societies particularly, construction may be a co-operative affair, requiring the co-ordinated and directive activity of a large number of workers. Such is the case, for instance, in the formation of the honeycomb by the hive bee. A not too fanciful analogy may be drawn between this co-operative building by worker bees and the construction of a bone by the activities of armies of chondroblasts and osteoblasts.

5. Constructive ability is shown in very high degree by man, and here we are on more familiar ground, for all his constructions are easily explicable in terms of physics and chemistry—and purpose. In the building of a house, for

example, materials of known physical and chemical properties, such as bricks, mortar, cement, wood, glass, metal pipes and so on, are assembled, shaped and put into position according to a plan thought out beforehand. In all this, no violence is done to the laws of physics and chemistry; on the contrary, knowledge of these laws is used to obtain the result aimed at, and the house when finished is a stable structure, adapted to fulfil its purpose by reason of the material properties of its constituent parts and their arrangement. But no one would dream of explaining the building of the house in terms solely of physics and chemistry. Human purpose must come into the story as an essential element. The building of a house is in fact a typical example of human purposive activity, arising out of a need or a desire, guided by forethought and a definite plan, which is adaptable to circumstances. The original plan may not be realised in the exact way intended; if slates are found to be too expensive or difficult to obtain tiles may be substituted, or if the ground is not so solid as expected extra foundations may have to be laid; but the end desired and planned will be reached, even though the means vary somewhat. There is persistence of effort until the end is reached, and, if necessary, variation in the method of attaining it.

The end is reached, the house is constructed, by utilising the physical and chemical properties of the materials, and by arranging these materials in a certain order. But the construction of the house can obviously not be explained in terms merely of the properties of the materials used. The same applies to the development of a living organism.

There is, of course, an enormous difference between development and human construction. In development there is no agent external to the organism, acting as builder or constructor. The organism constructs itself, makes, as it

were, its own bricks* and arranges them, utilising material and energy drawn from its own stores and from its environment. But there is common to development and construction the continuous ordering and arranging of the materials available, in such a way as to achieve a specific end-state of ordered, and, in the case of the living thing, organised, complexity. Development is a directive and creative process, aiming at, and often achieving, through material means, a specific functional organisation. The developing organism also shows in varying degree a power of regulation, so that the specific end-state may be reached by somewhat different ways.

No more than in the case of human construction can the development of a living organism be interpreted solely in terms of physical and chemical laws. Such an interpretation would leave out the essential thing, the directiveness of developmental activities, the ordering and arranging of materials to achieve a specific result. In development no physical or chemical law need be abrogated, any more than in the building of a house, yet development is not therefore reducible to, or explicable solely in terms of, physical and chemical laws. And it is obvious that we cannot have recourse to conscious purpose as an explanation of development. Nor does it really help to put the purpose inside the organism in the shape of an immaterial entelechy, which guides and controls development.

Now, regarded merely as a structural organisation, that is regarded abstractly as a physical and chemical mechanism, the living plant or animal is far more cunningly framed and far more elaborate than anything ever built

* Cf. Sherrington: 'The cell is an organised factory conducting manifold chemical processes. It hydrolyses, it pulls to pieces, it excretes. Further, it constructs. From bacterium to tree, from animalcule to man, proteins, broadly taken, are the stones of which the house of life is built. The cell makes its own proteins' (1940, p. 80).

by man. If we compare it with, say, an ocean liner or a bombing plane, we must admit that in far smaller compass life produces far greater organised complexity. The living tree is far more elaborate in its intimate structure (including its protoplasmic organisation) than any house or ship constructed of its wood. And the living organism is more than a mere structural organisation or mechanism; it is a functioning, self-regulating, self-maintaining and self-reproducing whole, a centre of directive activities which build up and maintain its complex organisation and functions. The developing organism itself produces, through its own directive metabolic and morphogenetic activities, the structural organisation which is essential to its functioning as a living individual. Constructive or creative activity of this kind is never shown by any machine, however elaborate, or by any inorganic system, however complex; it is something peculiar to, and characteristic of, life.

The development then of any highly organised being culminates in the production of a functional organisation that is far more complex than any machine or human construction and is in addition self-maintaining, adaptable and self-reproducing. Yet this comes about through the organism's own powers, in particular through the orderly activities of its cells, and we have no reason whatsoever to think that they act intelligently, with knowledge and foresight of the part they are to play in the development of the whole. All that we know leads us to suppose that they act more or less blindly, though not mechanically.

Here then is an apparent paradox. Through blind unconscious activities, which are orderly, co-ordinated, and directive towards specific ends, there is built up a functional organisation which is far more complex and perfect, both in its structure and its working, than anything man can

construct with the aid of his highest powers of intelligence and manipulative ability.* Directive and creative activity without foreknowledge of the end achieves far more striking results than the consciously purposive action of man, and by methods entirely different from those which he employs in making machines, or houses. Man makes the parts of his constructs separately and fits them together. The egg works from within outwards; it proceeds by growth and self-differentiation, based upon directive metabolic activity, taking from the outside only raw materials which it builds into its own substance; there is no fitting together of pre-fabricated parts. The more one considers the living organism and the manner of its development, the less machine-like does it appear.

This suggests that in assimilating the living thing to a machine, or more generally, to an ordered material configuration, with or without a guiding and regulating entelechy, we are taking quite the wrong direction. The difficulties of both the materialistic and the vitalistic conception are immense, and they all arise from acceptance of the hypothesis that the organism is an ordered configuration, or physico-chemical 'mechanism' in the wide sense—in principle similar to a machine of human construction. The vitalist puts the constructor and regulator inside the machine; the materialist conveniently ignores the orderliness and regulability of the organic machine. But machines are by-products of life, and the living thing is not really machine-like.

The fact is that in dealing with the activities that lead to the building up, the functioning and self-perpetuation of living organisms we enter upon a totally different world

* Cf. Schopenhauer: 'the organism presents itself as a miracle which admits of no comparison with any work of human artifice wrought by the lamplight of knowledge' (Parker, 1928, p. 404).

from the mechanical and machine-like, a world also in which the conscious purpose of the individual plays a very subordinate and exceptional role. Between the sphere of conscious purpose and the world of the inorganic and mechanical, there lies the vast realm of the organic, with its directive, creative and regulative activities. In this realm, as we have seen, action, whether it be behavioural, morphogenetic or physiological, is normally directive towards ends related to self-maintenance, development or reproduction, but only rarely is it consciously purposive; it is also creative, in each ontogeny, and in evolution, of new form, new organisation, new functional powers. There is nothing like this to be observed in the inorganic realm, and only a pale copy of it in the world of conscious purpose. An aeroplane is much inferior to a bird, a submarine to a whale, for the living organisms are not only more complex in their intimate organisation, but they are self-maintaining and self-regulating, independent of external control and guidance, and supplying their own fuel.

Actually there is no real paradox in the fact that life produces organisms of much greater complexity and self-sufficiency than any machine of human construction, for machines are merely the product of the purposive intelligence of one specialised organism, man, and his intelligence and purposive behaviour are dependent upon, and conditioned by, the directive and creative organic activities of his development.

That human thought, and science itself, are dependent on the directive and creative activities of life becomes very obvious when we consider the development of a human being. A human ovum, which is a cell of about 0.2 mm. in diameter, develops (if certain elaborate conditions are normal), through its own activities and according to a fixed routine of orderly changes, into the large and highly

organised body of an adult human being with its thousand billion cells (Sherrington, 1940, p. 104). In the course of this long process of development, extending over years, new structures, new organs, new powers, including mental powers, arise that were certainly not present in the beginning. There is therefore real creation or formation afresh of an organisation which renders possible functional and mental activities of which the organism in its earlier stages is incapable. A certain level of organisation must be reached before these activities can appear. The child cannot walk or talk until its neuro-muscular system attains a certain degree of organisation, nor can the adolescent develop his powers of thought until his brain 'matures'. Exercise and training help greatly in the development of these powers, but proficiency is in the main dependent on the morphogenetic processes which lead to the elaboration of a fully developed brain and nervous system in all its immense intricacy. Let us realise just what this means. It means that the power of conceptual thought, which is the basis of science, is dependent on, and conditioned by, the directive and creative activities of the developing body, which result in the building up of the incredibly complex and orderly organisation of the fully functional and normal adult human body, including normal sense organs, brain and neuro-muscular system. Without this elaborate organisation and certain environmental conditions, such as an adequate oxygen supply, thought is impossible. Developmental activities, though blind and unconscious, are therefore the prior condition of human thought, which is accordingly dependent upon these activities. This is a fact of immense importance, which has largely escaped the notice of philosophers. It is our human failing that we exalt our intelligence, which is derivative, over the organic activities that produce its necessary conditions, and attempt

to explain these activities in terms of limited and anthropocentric concepts, derived from our experience of acting upon material things. We should remember that intelligence is only a means to life, not life itself. Instead of attempting to explain the 'teleological' nature of organic activities in terms of concepts derived from man's knowledge of his own purposive activity, as do the mechanist and the vitalist, we should take precisely the opposite view, and regard human purposive activities (including machine-making) and modes of thought as being a specialised development of the fundamental 'purposiveness', or as I prefer to call it, the directiveness and creativeness, of life: If this be, as I maintain, the right view to take, then we must accept the 'teleological' nature of vital activities as something given and fundamental, not to be explained in terms either of physico-chemical action or of purpose.

That we cannot explain or account for the directiveness and creativeness of life need make no difference to our projected functional biology; we must simply accept the immanent teleology of organic activities as, so to speak, the basis or background of our biological thinking.

We are free then to trace out in detail how and to what extent organic structure and activities are related to the biological ends of living and perpetuating the species. We know already that the teleology of organic activities is, in the main, a limited and specialised teleology, that these activities may be stereotyped and not always purposive (see pp. 102-8), that they are subject to restrictive laws that can be ascertained. Because organic teleology is not mechanical, it is not therefore something miraculous and supernatural.

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THE CONCEPT OF ORGANISM

I. LIFE AND MIND

We have reached the conclusion that directiveness and creativeness are fundamental characteristics of life, shared by no inorganic system; that they are not to be explained in terms of mechanism or of purpose; that human directiveness and purposiveness in thought and action are a specialised development of the directiveness and creativeness inherent in life. If this be the true state of affairs, then it would seem that psychological activity issuing in purposive behaviour is to be regarded as a specialisation of vital activity. We have seen that, regarded from the point of view of functional biology, behavioural action on the part of organisms and cells is only one of the methods by which biological ends are reached, that it is functionally equivalent to morphogenetic and physiological action, that all three kinds of action show common characteristics, such as persistence of effort towards achieving the normal goal, cessation when this goal is reached, and that these modes of action may be functionally complementary or even substitutionary. All this suggests that organic and psychological activities are closely akin. We must not, however, make the mistake of regarding psychological activity as prior to organic activity in general, nor must we attempt to explain organic activity in psychological terms applicable primarily to human behaviour. The fact is that the common ground of both organic and psychological activity lies in the directiveness or 'drive' which is characteristic of both.

We must regard directiveness as an attribute, not of mind but of life. Instead of drawing an absolute distinction between matter and mind, and accepting that 'dichotomy of Nature' which the genius of Descartes imposed for so long upon human thought, we shall draw the line, for the practical purposes of functional biology, between organic activity and inorganic, and with organic activity we shall include, as one of its modes, behavioural or psychological activity. We recognise the fact that organic activities, as manifested by organised unities such as cells and organisms, show characteristics, especially their directiveness, persistency and adaptability, which are shown also in the instinctive and intelligent behaviour of ourselves and other animals. But we shall not fall into the error of interpreting organic activities in general in terms of conscious purpose or 'mind'. Rather shall we take the view that purposive activity, as seen in its highly developed form in the intelligent behaviour of man, is a specialised and elaborated kind of directive activity, concerned mainly with the mastery of his material environment.

From this new point of view, we can no longer think of the living organism as a physico-chemical mechanism, with or without a guiding mind, but as an organic unity or agent, showing directive modes of activity, some of which may become, as in man, consciously purposive. We draw no hard and fast line between organic and psychological activity; there is for us no mysterious 'emergence' of mind from purely material organisation, either in evolution or in individual development, nor are we concerned with the insoluble question of the relation of mind to matter. We have to deal simply with the modes of action of organic units or agents, some of which modes may be psychological. In this view I follow C. S. Myers (1932), who holds that life and mind are at bottom the same.

'Mind and life', he writes, 'are identical properties of what we term living matter*—a peculiar form of activity, differing from that of lifeless matter, in the inherent purposive, self-directive, and finally purpose-felt struggle for existence' (p. 9).

Only by adopting this view can we avoid splitting biology into a mechanistic physiology on the one hand and psychology on the other, and perpetuating what McDougall has called 'the intolerably absurd state of affairs hitherto obtaining; namely, two sciences of the functioning of organisms, on the one hand mechanical biology, on the other psychology; two sciences completely out of touch with one another; the one ignoring the mental life of men and animals, the other trying vainly to relate it intelligibly to the bodily life' (1938, p. 265).

McDougall goes on, making the point, which we have tried to illustrate in previous sections, of the functional equivalence and complementariness of different modes of action: 'Animal life presents thousands of instances in which the animal's building of its bodily structures or appendages and its building of external structures with foreign material, go on in most intimate co-operation as complementary parts of one process; and the outer building, being what we call instinctive activity, presents all the essentials of a mental or psychical activity; while the same essential marks are presented, though more obscurely, by the morphogenetic processes which build the body and its organs; namely, in both cases the activities are teleological (obstinately persisting towards the specific goal), are intelligently adaptive in high degree (reverting to and restoring normality after disturbances), and yet in both cases they are mnemic, striving to repeat, to reproduce the pattern common to the species, the pattern impressed

* I should prefer to say 'living units' or agents.

upon it by countless repetitions of essentially the same course of activity. I have in mind more particularly such activities as the building of cocoons or other cells for the harbouring of the creature. The two kinds of construction often go on in strictly supplementary fashion, each implying and requiring the other. And in many such cases it is clear that the bodily movements or behaviour and the growth processes are alike partial responses of the whole organism to the same impressions or environmental influence; as when a fall of temperature provokes both a growth of hair and retreat to some sheltered spot' (p. 266). Morphogenetic activities and instinctive are linked, complementary, and functionally equivalent, and resemble one another in their essential characteristics.

2. THE CARTESIAN DICHOTOMY

Most of the theoretical difficulties of biology arise from a blind acceptance of the Cartesian dichotomy of matter and mind. This works admirably in the physical sciences, where life and mind do not come into the story. Applied to living things it leads inevitably to the conclusion that they are nothing but energy systems, that, as Sherrington puts it, the difference between the living system and the inorganic system 'is one not of ultimate nature but of scheme and degree of complexity' (1940, p. 85). The rock, and the dragonfly that circles above it, as pure energy systems, fall into one category, and all the faculties or functions of the cell are processes 'which examination resolves wholly into chemistry and physics' (p. 86).

It is of course perfectly possible to take such a view of the relation between organic and inorganic systems, to regard them as essentially the same in kind and differing only in degree of complexity, and so to reduce biology to biophysics and biochemistry. But to do so is to neglect the

distinctive characteristics of organic systems, as self-maintaining, self-regulating, developing and reproducing organisms. The category of energy system is too wide and all-embracing. Sherrington himself brings out the orderliness and directiveness of the physico-chemical processes underlying the life of the cell. 'Our conceptions of it', he writes, 'fail if not dynamic. It is a scene of energy-cycles, suites of oxidation and reduction, concatenated ferment-actions. It is like a magic hive the walls of whose chambered sponge-work are shifting veils of ordered molecules, and rend and renew as operations rise and cease. A world of surfaces and streams. We seem to watch battalions of specific catalysts, like Maxwell's "demons", lined up, each waiting, stop-watch in hand, for its moment to play the part assigned to it, a step in one or other great thousand-linked chain process. Yet each and every step is understandable chemistry' (p. 78). And again: 'In the sponge-work of the cell foci coexist for different operations, so that a hundred, or a thousand different processes go forward at the same time within its confines. The foci wax and wane as they are wanted. That the cell's field is a colloidal field makes explicable much which would otherwise not be so. But the cell is much more than merely a drop of colloidal jelly. The processes going forward in it are co-operatively harmonized. The total system is organised. The various catalysts work as co-ordinately as though each had its own compartment in the honeycomb and its own turn and time. In this great company, along with the stop-watches run dials telling how confreres and their substrates are getting on, so that at zero time each takes its turn. Let that catastrophe befall which is death, and these catalysts become a disorderly mob and pull the very fabric of the cell to pieces. Whereas in life as well as pulling down they build, and build to a plan' (p. 79).

It may be true that, as he says, 'each and every step is understandable chemistry', but what of the orderliness in time and space of these steps? Surely the difference between an inorganic and an organic system lies not in the greater complexity of the latter, but in the orderly directiveness of its activities towards the ends of living, developing and reproducing? If we treat them both as energy systems differing merely in complexity, we leave out what is distinctive of the organic system. But why disregard the vast differences between the living and the not-living, the directiveness, orderliness, adaptability and creativeness of organic activities, which are so patent and obvious characteristics of living systems, and lacking in the inorganic world?

We have already pointed out that the causal-analytical method of the physical sciences, applied strictly to the activities of life, leads only to analysis without end, and that though we may adequately describe details, or even 'each and every step', in physico-chemical terms, this knowledge means nothing *biologically*, unless we can link up the details with the life of the organism as a whole. We do require this distinctively biological understanding of the details in addition to a knowledge of their physico-chemical 'mechanism', and this means that we must take into account the directiveness and orderliness of organic activities, and even of the physico-chemical processes underlying the functions of the cell, as essential and unique characteristics of vital activity.

An analogy may be taken from artistic production and appreciation. A painting is, from the point of view of physico-chemical science, simply an arrangement of pigments, the chemical nature of which can be ascertained. But we might know in full detail everything about the chemical composition of the pigments and the pattern of

their arrangement without in the least understanding or appreciating artistically the picture as a whole. And we should not be able, from the strictly physico-chemical point of view, to form any conception of how the particular arrangement of pigments came into being. The analogy is admittedly a loose one, for artistic appreciation is not the same as intellectual understanding, and the painting is merely a static 'construction', and not a living organism; but a purely physico-chemical treatment of the living thing pursued to the bitter end, without considering the biological significance of the separate processes of mechanisms discovered by analysis, would yield little more understanding of the living thing than a physico-chemical analysis does of the picture.

The conception of the organism as a pure energy system derives, as we have said, from an acceptance of the Cartesian dichotomy of matter and mind. If we accept the absolute separation, as different in nature, of matter and mind, we cannot possibly put them together again in any understandable relation; we cannot see how mind can possibly influence matter, and we are in practice driven to a purely physico-chemical or materialistic treatment, not only of inorganic things, but of living organisms also. We are precluded from any psychological or psychobiological treatment of the activities of life; a purely material system cannot, *ex hypothesi*, perceive, strive or act purposively.

Yet our own experience shows us, beyond a shadow of a doubt, that at least one organism does perceive, strive and act, and there is strong evidence, from their behaviour, that many other organisms also possess these distinctively psychological functions or powers. It follows then that the conception of the organism as a purely material system is faulty and inadequate. For the purposes of functional

biology we must reject the antithesis of matter and mind, which are purely abstract conceptions, and recognise that psychological activities are characteristic of at least some organisms, that such activities are a function of living organism and not of a fiction called 'mind'.

But, as has been indicated above, we go considerably beyond the mere recognition that psychological activities are shown by some living organisms; we maintain that there is a common root or ground for both psychological and other vital activities in their directiveness towards biological ends and that this is the very essence of life.

3. THE CONCEPT OF ORGANISM

We may return now to the point made at the beginning of this book (p. 3), that the central concept of functional biology must be organism, not mechanism. The mechanistic conception of the living organism being inadequate and restrictive, it is necessary to replace it by a more realistic conception, which shall take account of the fundamental or irreducible characteristics of living things, those, namely, which are shown by no inorganic system, and without which no living organism is conceivable, characteristics therefore which cannot have arisen during the course of organic evolution, for life of any degree presupposes them.

I have pointed out that directiveness and creativeness are such characteristics, and I have indicated in some detail in the course of this book the directive and creative nature of organic activities, whether they be behavioural, morphogenetic or physiological. Both characteristics are manifest even in the physico-chemical activities of the living cell, which is a centre of organised, orderly physico-chemical actions directive towards the building up and maintenance of its structuro-functional organisation and

the performance of its proper functions. The directive and orderly nature of the myriad processes going on in the living cell we have seen well illustrated by Sherrington (1940) in the passages quoted above on p. 182. Without such orderliness, directiveness and creativeness the activities of the cell fall into chaos; disintegration and death follow at once.

We have seen that the activities of the organism and of its subordinate parts are directive towards the biological ends of living, developing and reproducing, towards the completion of a normal life-cycle. It is as a life-cycle progression and not as a static organisation that the living thing is ultimately to be conceived. I may recall here the statement of this fundamental point reproduced above (pp. 5-7) from my 1934 Address, and requote the summing up: '...the living organism has characteristics which are lacking in inorganic systems, and it can be adequately defined or characterised only by reference to those peculiarities which we have just considered—the weaving together in one cyclical process of the master functions of maintenance, development and reproduction. These distinguish it from any inorganic object or construction, from any inorganic system. Underlying these characteristics is the general directiveness of its activities, their constant drive towards a normal and specific end or completion.'

Now for an organism to live and complete its life-cycle successfully certain conditions must be fulfilled. It must actively maintain its structuro-functional integrity, and it must satisfy its essential needs and requirements. To do so it must inhabit an environment which is functionally correlative with its particular needs and requirements for maintenance, reproduction and development. It must, in a word, be integrally adapted to its environment, or series of environments, throughout its whole life-cycle.

Let us consider these two conditions of existence in more detail. The first condition is that the organism must maintain and preserve its structuro-functional integrity and wholeness as a 'going concern', at all stages of its life-cycle. It must be capable of carrying out in an integrated and orderly way the physiological activities of respiration, assimilation, excretion and the like, which are essential for active life; it must be capable of appropriate action, by behaviour or morphoplastic process, that it may find food, or light, or support, or escape from its enemies. This implies an adequate degree of morphological integrity or wholeness, for life is dependent upon organisation. It is then a primary condition of its active existence that the organism must be a harmoniously working structuro-functional unity, capable of performing the metabolic and other functions which are essential to its life.*

Now for the vital metabolic functions to continue, the organism must be able to satisfy its essential metabolic needs. The metabolic processes which are basic to life cannot continue indefinitely unless the organism draws material and energy from without. It needs food material of some kind, water, oxygen, light in the case of green plants, and a number of special substances, and all these it must obtain in the long run from its environment.

What is true of its metabolic needs is true also of all its other needs and requirements, not only for maintenance but for development and reproduction. Accordingly, stating the matter in its most general terms, we may say that the organism is dependent upon its environment for the satisfaction of its vital needs and requirements through-

* This is what Cuvier emphasised as the essential 'condition of existence' (see my *Form and Function*, 1916, p. 34). 'Conditions of existence' in the sense introduced by Charles Darwin meant environmental conditions only (*ibid.* p. 239).

out its whole life-cycle; these needs may change in the course of its life, the needs and requirements for reproduction may be different from those for maintenance, those for the egg and larva different from those of adult life, and the appropriate environment must change also. But at all stages the environment must be suitable or adequate.

That is what 'adaptation to environment' means from the point of view of functional biology. An organism is adapted to its environment when it can satisfy in that environment all its essential needs and requirements for maintenance, reproduction and development; if it be not so adapted, it cannot exist as an individual or persist as a species. Adaptation to environment is then a primary condition of existence of every living creature.

Now adaptation to environment necessarily implies some degree of specialisation. Environments are highly diversified, and there is, or can be, no such thing as a generalised organism, capable of active existence and reproduction in all kinds of environment in which life is possible at all. Living organisms, as we know them, are all of definite kinds, each kind specialised in diverse degree for a particular mode of life in a more or less restricted environment, and this clearly must be so, and must always have been so, from the very dawn of life. The first living things were no doubt very simple in organisation, but they must have been integrally adapted to their environment, otherwise they could not have existed; they must also have been specialised in some degree. We may conclude therefore that a primary condition of existence of any organism, even the simplest, is its adaptation to environment—its adaptedness to, that is, its viability within, a more or less specialised environment which is correlative with, and capable of satisfying, the essential needs and requirements of the organism throughout its life-cycle.

Adaptation to environment is not something which has arisen during the course of organic evolution. To be capable of evolutionary change, organisms must be viable, and to be viable they must already be adapted to environment (and to some degree, specialised). While therefore the innumerable diverse forms of adaptively specialised organisms which have appeared in the history of the globe owe their existence to an evolutionary process, the factors and causes of which may be discovered, the fact remains that the very earliest forms of life, to exist and persist at all, must themselves have been adapted to their environment, for this is the very condition of their existence.

It was the fashion, in the heyday of evolutionary speculation, to postulate the existence in the past of primitive and generalised ancestral forms, bearing a curious resemblance to the 'archetypes' of pre-evolutionary morphology—a sort of abstract or extract of the essential morphological features of the type. But these hypothetical beings could never have been viable; they were purely fictional organisms, incapable of life or of making a living, because they were not adaptively specialised.*

Evolutionary diversification obviously cannot proceed unless the essential conditions for living and reproducing are present from the beginning. Of these conditions adaptation to environment is one, and it cannot have arisen in the

* Even so good a naturalist as Minchin seemed to regard the animal as a more or less 'neutral' organisation, on which are imposed, or to which are added, adaptive characters related to special needs or environmental conditions. 'There is probably no living organism', he wrote, 'which does not possess some special features, owing their existence to the fact that they are of utility to the organism in its efforts to maintain and perpetuate its existence in the way in which its environment requires' (1898, p. 563). There is no recognition here of the fact that the animal must be integrally adapted and specialised as a whole if it is to exist and persist at all. The concept of integral adaptation was brilliantly expounded by Schopenhauer more than a century ago in the section on Comparative Anatomy in his book *Ueber den Willen in der Natur* (1836).

course of organic evolution, for evolution presupposes it. (We are not concerned here with the purely hypothetical evolution of living organisms from inorganic matter.)

Primary characteristics of the living organism are then the directive, creative and orderly nature of its activities in relation to maintenance, reproduction and development, to the completion of the normal life-cycle; primary conditions of existence are the preservation of structuro-functional wholeness or normality, and integral adaptation to an environment (or series of environments) in which the particular needs and requirements of the organism for the completion of its life-cycle can be satisfied.

It is important to note that the conditions of existence must be *actively* established and maintained. Structuro-functional wholeness or integrity, and specific structure, are actively built up and maintained in the course of development, chiefly by the morphogenetic and behavioural activity of cells or groups of cells. If this integrity is disturbed by injury or by adverse environmental influences, it is, so far as possible, restored by appropriate physiological, behavioural or morphogenetic activities on the part of the organism and its cells, so that the normal state is restored or a new adaptive norm of structure and function is set up. The organism actively seeks out and selects the substances necessary for its metabolism, or draws them from its stores. It actively seeks in many cases its appropriate environment, and strives to maintain itself therein; it actively seeks in many cases a suitable ecological niche for its eggs and offspring. In all these ways, and in many others, the organism strives to persist in its own being, and to reach its normal completion or actualisation. This striving is not as a rule a conscious one, nor is there often any foresight of the end, but it exists all the same, as the very core of the organism's being.

This view of the living organism was clearly expressed

by Spinoza in 1677 in the famous sentence 'Conatus, quo unaquaeque res in suo esse perseverare conatur, nihil est praeter ipsius rei actualem essentiam', which may be rendered thus: 'The effort by which each thing endeavours to persist in its own being is nothing else than the actual essence of the thing itself.' As Mrs Arber points out in a thoughtful article on plant morphology, Spinoza set the principle of self-maintenance 'in the fore-front of biology, by making the urge towards self-maintenance, not merely a character of living things, but the very gist of life' (1941, p. 81). And the drive or conatus covers more than mere maintenance. It is not possible to separate the drive to self-maintenance from the developmental drive, or drive towards completion, for the life of an organism is always a progression, a movement towards the fulfilment of the normal life-cycle; self-maintenance is there 'for the sake of' the completion of the life-cycle. To quote Mrs Arber again: 'The endeavour to persevere in its being means more than may be recognized at first glance. It implies the endeavour to bring the "*determinata natura*" of that being into a condition of completeness or perfection in its own kind' (p. 86). A drive towards the actualisation of potentialities, to which self-maintenance is a means, perhaps describes more accurately the essence of individual life—in Aristotelian phraseology, a movement from *δυνάμεις* or potentiality to *ἐντελεχεία* or actualisation, 'the perfect realization of all that any creature or power is capable of becoming' (Hett, 1935, p. xi; on Aristotle's concept of entelechy, see also Ritter, 1932, 1934).

This drive is not normally a conscious one, and confusion is apt to arise because to characterise it we have no other words than those which carry a psychological meaning, words such as 'effort', 'perseverance' and 'urge', which are primarily applicable to human behaviour. Mrs Arber has called attention to this difficulty, but holds, quite

rightly, that the use of such words is unavoidable, 'because we have no other set of terms in which to express that compulsiveness by which the plant works towards a certain end, which, if we were concerned with a self-conscious organism knowingly pursuing a train of activity, would be recognized as a goal' (1941, p. 87). We really require new terms to characterise the goal-directed and biologically purposive activities of living organisms, of which only some reach the level of conscious purposiveness.

Our conclusion that life processes are essentially and fundamentally directive and creative may be rejected as 'metaphysical' or 'mystical'. It is of course nothing of the sort. I make no hypothesis as to the philosophical basis or 'ground' of directiveness and creativeness. I merely accept the patent evidence that they are characteristic of living things and of them alone. Nor do I suggest anything strange in the way of method. I suggest simply that, instead of making continual and vain efforts to squeeze biological facts within the materialistic frame, and attempting analysis without end, we accept them *as biological*, that we deal with the problems of development, maintenance and reproduction in terms of the observable activities of the organic agents concerned, without making the gratuitous hypothesis that these activities are mechanistic. Only in this way can we hope to establish the laws of organic activity.

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